Journal of Systematic Palaeontology
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tjsp20

Postcranial axial skeleton of Europasaurus holgeri (Dinosauria, Sauropoda) from the Upper Jurassic of Germany: implications for sauropod ontogeny and phylogenetic relationships of basal Macronaria

José L. Carballido [a b] & P. Martin Sander [a]

[a] Steinmann Institute, Division of Palaeontology, University of Bonn, Nussallee 8, 53115 Bonn, Germany

[b] Consejo Nacional de Investigaciones Científicas y Técnicas; Museo Paleontológico Egidio Feruglio, Fontana 140, 29100 Trelew, Argentina

Version of record first published: 25 Mar 2013.

To cite this article: José L. Carballido & P. Martin Sander (2013): Postcranial axial skeleton of Europasaurus holgeri (Dinosauria, Sauropoda) from the Upper Jurassic of Germany: implications for sauropod ontogeny and phylogenetic relationships of basal Macronaria, Journal of Systematic Palaeontology, DOI:10.1080/14772019.2013.764935

To link to this article: http://dx.doi.org/10.1080/14772019.2013.764935

Journal of Systematic Palaeontology, 2013
http://dx.doi.org/10.1080/14772019.2013.764935

Postcranial axial skeleton of *Europasaurus holgeri* (Dinosauria, Sauropoda) from the Upper Jurassic of Germany: implications for sauropod ontogeny and phylogenetic relationships of basal Macronaria

José L. Carballido[a,b]* and P. Martin Sander[a]

[a]*Steinmann Institute, Division of Palaeontology, University of Bonn, Nussallee 8, 53115 Bonn, Germany;* [b]*Consejo Nacional de Investigaciones Científicas y Técnicas; Museo Paleontológico Egidio Feruglio, Fontana 140, 29100 Trelew, Argentina*

(Received 29 May 2012; accepted 10 September 2012)

Neosauropods are well represented in the Late Jurassic fossil record, both in Laurasia and Gondwana. Among Macronaria, *Europasaurus* represents one of the most basal forms of this group. In addition to its systematic importance, *Europasaurus* is also the first unequivocal dwarf sauropod from which adult and juvenile material is available. Despite the abundance of sauropods in the fossil record, early juvenile specimens are rare, limiting knowledge about sauropod ontogeny. Therefore, the great amount of material of *Europasaurus* provides an excellent opportunity to improve our knowledge on the early evolution of Macronaria, as well as to shed light on some morphological changes through ontogeny. The postcranial axial skeleton of sauropods is extremely modified with respect to the anatomy observed in its ancestors, the 'prosauropods', proving to be one of the most informative regions of the body. Here we provide a detailed description of the axial skeleton of *Europasaurus*, including adult and juvenile elements, discussing its systematic and ontogenetic importance. We also analyse the phylogenetic position of *Europasaurus* through a cladistic analysis using TNT, which retrieves this taxon in a basal position among Camarasauromorpha. Additionally, the presence/absence of discrete characters and the comparison of juvenile elements with adult specimens allowed us to recognize different morphological ontogenetic stages (MOS). Whereas early stages lack derived characters (e.g. spinodiapophyseal lamina and prespinal lamina on dorsal vertebrae), all derived characters (including autapomorphies) are present in late immature specimens. Therefore, while late immature specimens provide the same phylogenetic signal as adult specimens of *Europasaurus*, more immature stages are recovered in a basal position among sauropods. Finally, we apply the MOS to other maturity criteria (e.g. neurocentral closure, sexual maturity) in a search for a wider definition of maturity.

Keywords: Macronaria; ontogeny; maturity; phylogeny; dimorphism; Late Jurassic

Introduction

Sauropod dinosaurs first appear close to the Triassic/Jurassic boundary (Buffetaut *et al.* 2000; Yates & Kitching 2003), and since this time they became the dominant terrestrial megaherbivores through all of the Mesozoic. During the Middle to Late Jurassic, this group experienced a great diversification, establishing the major lineages of Neosauropoda (Upchurch 1998; Wilson & Sereno 1998; Wilson 2002; Upchurch *et al.* 2004; Carballido *et al.* 2011b; Mannion *et al.* 2011b; Upchurch *et al.* 2011). Most of these forms are represented by taxa from the Late Jurassic of western North America (e.g. *Camarasaurus*, *Brachiosaurus*, *Diplodocus*; Cope 1877; Riggs 1903; Marsh 1878; Madsen *et al*. 1995; Taylor 2009), Tanzania (e.g. *Giraffatitan*, *Torneria*, *Australodocus*; Janensch 1914; Fraas 1908; Remes 2007; Taylor 2009) and Portugal (e.g. *Lourinhasaurus*, *Dinheirosaurus*, *Lusotitan atalaiensis*; Lapparent & Zbyszewski 1957; Antunes & Mateus 2003; Mannion *et al.* 2012).

Europasaurus holgeri represents one of the more recently described basal camarasauromorphs from the Late Jurassic (middle Kimmeridgian). Since its first preliminary description (Sander *et al.* 2006), *Europasaurus* has been considered as a basal camarasauromorph (*sensu* Upchurch *et al.* 2004) less derived than *Brachiosaurus*, a position subsequently recovered by other authors (Carballido *et al.* 2011a, b). Therefore, this taxon is of great interest for improving our knowledge of the anatomy, early evolution and radiation of basal camarasauromorphs. In addition, *Europasaurus* was shown to be an unequivocal dwarf sauropod (Sander *et al*. 2006) in a lineage of gigantic forms such as *Brachiosaurus*, *Tehuelchesaurus* and *Argentinosaurus* (Stein *et al.* 2010; Klein *et al.* 2012). The dwarf condition of *Europasaurus* opens a great number of questions, mainly related to the evolutionary process that led to the evolution of such forms.

Despite the abundance of sauropods in the fossil record, they are mainly represented by adult and subadult individuals; juvenile specimens are rare (e.g. Foster 2003; Ikejiri *et al.* 2005; Tidwell & Wilhite 2005). Consequently,

*Corresponding author. Email: jcarballido@mef.org.ar

knowledge of sauropod ontogeny remains limited, especially for early ontogenetic stages. This is particularly unfortunate because no other amniotes grew through the same size range from neonate to adult as did sauropods (Sander *et al.* 2008; Griebeler & Werner 2011; Werner & Griebeler 2011).

A few remarks are in order about the nature of the *Europasaurus* fossil material (see also Sander *et al.* 2006). Skeletal preservation ranges from partially articulated skeletons and associated skeletons, to isolated bones. Sometimes the state of articulation and association is difficult to determine because the bones were not found by palaeontological prospecting and excavation but were discovered in the fracture planes of blocks of host sediment freed by blasting from a steep quarry face. Commonly, originally complete bones are fractured, and only some parts can be recovered from the rubble. In addition, the exact nature of the bone becomes apparent only after preparation, and parts of the same bone may be joined years after their discovery. Among the tons of rocks removed from the quarry producing *Europasaurus* and the thousands of elements catalogued as *Europasaurus holgeri* at the Dinosaurierpark Münchehagen (DFMMh), several juvenile remains were found. Although disarticulated, this juvenile material gives us a great opportunity to understand some of the changes that sauropods underwent during their ontogeny. Such changes can only be recognized after a detailed revision and comparison of the anatomy of both mature and immature specimens.

Unlike most other tetrapod lineages, the postcranial axial skeleton of sauropods has proven to be one of the most informative regions of the body (Bonaparte 1999). The axial skeleton of sauropods is extremely modified with respect to the anatomy observed in basal sauropodomorphs. These modifications mainly consist of the evolution of a complex arrangement of laminae and fossae, the nomenclature and homology problems of which are continually being discussed (e.g. Bonaparte 1999; Wilson 1999; Apesteguía 2005; Salgado *et al*. 2006; Salgado & Powell 2010; Wilson *et al.* 2011).

Here we describe in detail the postcranial axial skeleton of *Europasaurus holgeri*. The description of juvenile specimens and their comparison with adult forms reveals some of the major ontogenetic transformations in the life history of *Europasaurus* in particular, and sauropods in general.

Material and methods

Abbreviations

Anatomical abbreviations. **ACDL**: anterior centrodiapophyseal lamina; **aml**: anterior median lamina; **ACPL**: anterior centroparapophiseal lamina; **cp**: capitulum; **cpof**: centropostzygapophyseal fossa; **CPOL**: centropostzygapophyseal lamina; **CPRL**: centroprezygapophyseal lamina; **cf**: condiloid fossa; **dp**: diapophysis; **epi**: epipophysis; **for**: foramen; **hypa**: hypantrum; **hypo**: hyposphene; **TPRL**: intraprezygapophyseal lamina; **lCPOL**: lateral centropostzygapophyseal lamina; **lprf**: lateral fossa of the prezygapophyseal process; **mCPOL**: medial centropostzygapophyseal lamina; **mdCPOL**: medial division of the centropostzygapophyseal lamina; **mdCPRL**: medial division of the centroprezygapophyseal lamina; **nc**: neural canal; **ntch**: notch; **oars**: odontoid articulation surface; **PPDL**: paradiapophyseal lamina; **pp**: parapophysis; **ped**: pedicels; **pl**: pleurocoel; **plr**: pleurocoel ridge; **pSPDL**: posterior spinodiapophyseal lamina; **PCDL**: posterior centrodiapophyseal lamina; **POSL**: postspinal lamina; **posc**: postspinal scar; **poz**: postzygapophysis; **PODL**: postzygodiapophyseal lamina; **PRSL**: prespinal lamina; **prsc**: prespinal scar; **prz**: prezygapophysis; **PRDL**: prezygodiapophyseal lamina; **scy**: sacricostal yoke; **sTPOL**: single intrapostzygapophyseal lamina; **sTPRL**: single intraprezygapophyseal lamina; **SPOL**: spinopostzygapophyseal lamina; **SPRL**: spinoprezygapophyseal lamina; **tb**: tuberculum; **TPOL**: intrapostzygapophyseal lamina.

Institutional abbreviations. **CM**: Carnegie Museum of Natural History, Pittsburgh, PA, USA; **CLH** Cuesta Lonsal Herrero, Galve, Spain; **DFMMh**: Dinosaurier-Freilichtmuseum Münchehagen/Verein zur Förderung der Niedersächsischen Paläontologie (e.V.), Germany; **FMNH**: Field Museum of Natural History, Chicago, IL, USA; **HMN-MB**: Humboldt Museum für Naturkunde, Berlin, Germany; **IVPP**: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MACN**: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; **MNN GAD**: Musee National du Níger, Níger; **PMU**: Palaeontological Museum, Uppsala, Sweden.

Terminology

Fossae and laminae. Fossae nomenclature is based on the landmark bipartite and tripartite system recently proposed by Wilson *et al.* (2011). For lamina nomenclature, we follow the scheme proposed by Wilson (1999) with the addition of a few laminae recently defined by other authors (Apesteguía 2005; Salgado & Powell 2010). Here we provide a brief discussion of some definitions in order to clarify the meaning of these names. Although most of the time the laminae are connected to the landmarks (e.g. parapophysis, diapophysis, zygapophyses), several modifications of this more basic pattern are observed in sauropods, and some laminae are not directly connected to any landmark. When this happens there are two main options: (1) use a new name to refer to it; or (2) choose one of the previously defined names. In the case of some laminae observed in *Europasaurus*, we chose the second option, as was recently suggested by Wilson & Upchurch (2009). Thus, these laminae are interpreted mainly based on their position and approximation to the landmarks.

Centropostzygapophyseal lamina. Apesteguía (2005) differentiated the centropostzygapophyseal lamina (CPOL) of Wilson (1999) into two different laminae, both present in dorsal vertebrae. These laminae are the medial CPOL (mCPOL) and the lateral CPOL (lCPOL). The paired mCPOL were distinguished from the lCPOL because they contact the medialmost region of the postzygapophysis and laterally bound the neural canal in dorsal vertebrae (Apesteguía 2005). In contrast, the lCPOL is developed as a paired lamina, which runs from the centrum to the lateroventral aspect of the postzygapophysis. Although Apesteguía (2005) mainly focused his discussion on dorsal vertebrae, the lCPOL originates in cervical vertebrae and persists to the anteriormost dorsal vertebrae. Apesteguía (2005) mentioned that the mCPOL first appears in anterodorsal vertebrae, when the lCPOL becomes reduced. In a few taxa, during the transition from one lamina to another, both laminae are present at the same time (e.g. *Camarasaurus*; Osborn & Mook 1921). Therefore, contrary to the lCPOL, the mCPOL is only present in dorsal vertebrae.

Medial division of the CPOL. The medial division of the CPOL (mdCPOL) originates from the presence of paired posterior fossae below the postzygapophyses (the CPOF; Wilson *et al.* 2011). This paired fossa is usually absent in dorsal vertebrae of most sauropods (e.g. *Camarasaurus*, *Ehuelopus*, *Europasaurus*; Osborn & Mook 1921; PMU 234; see below). As a result of these fossae, the lCPOL becomes divided, forming a dorsomedially oriented lamina, which does not contact the postzygapophysis dorsally but contacts the TPOL. This lamina is referred to here as the mdCPOL. Although it can be confused with the mCPOL (described above), this lamina does not contact the postzygapophyses and is therefore not homologous to the mCPOL present in dorsal vertebrae, and thus a different name is advisable.

Medial division of the CPRL. This lamina is the anterior counterpart of the mdCPOL, and is generally present in the anterior view of cervical vertebrae. As with the mdCPOL, it arises from the presence of paired anterior fossae (the CPRF of Wilson *et al.* 2011), which are present in several taxa (e.g. *Diplodocus*, *Camarasaurus*). This lamina does not represent the divided CPRL of Upchurch (1995, 1998, character 88; Upchurch *et al.* 2004, character 113) or Wilson (2002, character 88) but the divided corporozygapophyseal lamina of Harris (2006, character 116). In contrast to the divided CPRL of Wilson (2002), the mdCPRL does not contact the prezygapophysis dorsally but instead the paired TPRL. Whereas the mdCPRL was recovered as a widespread character in sauropods (Harris 2006), the divided CPRL was recovered as a synapomorphic character of diplodocids (Wilson 2002), convergently acquired in Nigersaurinae (Whitlock 2011).

Intrazygapophyseal laminae. The definitions of the intraprezygapophyseal lamina (TPRL) and intrapostzygapophyseal lamina (TPOL) are not modified here. Instead, we refer to the single lamina formed below the median contact of these laminae as the single intrazygapophyseal lamina (sTPRL or sTPOL). Both laminae are normally present in cervical vertebrae but disappear in anterodorsal vertebrae, persisting only in the anteriormost dorsal elements (e.g. *Camarasaurus*). The sTPOL persists in middle and posterior dorsal vertebrae of diplodocid sauropods (Wilson 2002; Upchurch *et al.* 2004) and, convergently, in *Tehuelchesaurus* (Carballido *et al.* 2011b). Wilson (1999) referred to it as a median strut, and Upchurch *et al.* (2004, character 146) called it the single lamina below the hyposphene. To clarify its origin and to facilitate the description, we refer to these laminae as single TPRL (sTPRL) and single TPOL (sTPOL).

Spinodiapophyseal lamina. Wilson (2002) defined the spinodiapophyseal lamina (SPDL) as the lamina that runs from the diapophysis up to the neural spine. Although this topological criterion makes the recognition of the lamina easy, two different origins for the SPDL were recently suggested by Salgado & Powell (2010). These authors distinguished two different SPDL, anterior (aSPDL) and posterior (pSPDL), a practice that is followed here, recognizing them by their different positions on the transverse process.

Pleurocoel. The term pleurocoel was never rigorously defined (Wedel 2003). Wedel (2003) used the term lateral pneumatopore instead of pleurocoel, defining it as the communication between the lateral aspect of the centrum and the internal air spaces. However, the presence of a pleurocoel was identified in more basal forms (e.g. *Patagosaurus*; Bonaparte 1986), in which no internal air spaces are present (e.g. Wilson 2002; Upchurch *et al.* 2004). Therefore, a broader definition is used to address systematic problems, and thus the term pleurocoel could be differentiated from the term pneumatopores, and the presence of one does not necessarily imply the presence of the other. Thus, for us a pleurocoel is a lateral excavation with well-defined anterior, ventral and dorsal margins (as is observed in cervical and anterodorsal vertebrae of *Patagosaurus*; PVL 4170). The posterior margin of the pleurocoel (as defined) is usually well marked, but sometimes it is gently excavated without a well-defined edge. As was defined by Wedel (2003), the pneumatopores can be recognized inside the pleurocoel, establishing communication between the pleurocoel and the internal pneumatic cavities (when present). Moreover, the pneumatopore can be absent, as is mainly observed in some basal forms (e.g. *Patagosaurus*; PVL 4170), in which the pleurocoel does not open into internal cavities or camerae.

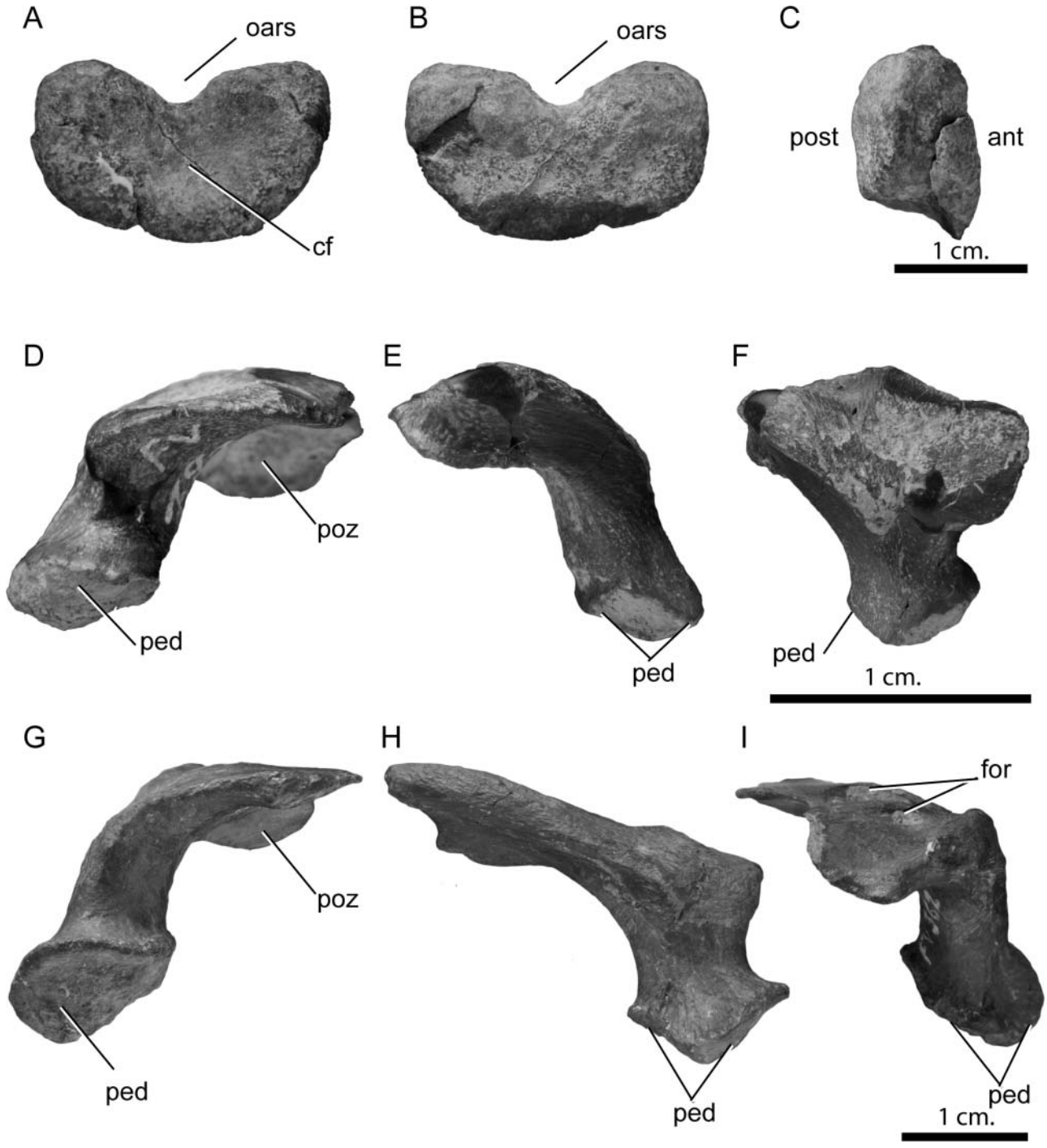

Figure 1. *Europasaurus holgeri*, atlas elements. **A–C,** intercentrum (DFMMh/FV 910) in **A,** anterior, **B,** posterior and **C,** lateral views. **D–F,** atlas neurapophysis (DFMMh/FV 791) in **D,** anterior, **E,** lateral and **F,** posterior views. **G–I,** atlas neurapophysis (DFMMh/FV 362) in **G,** anterior, **H,** lateral and **I,** posterior views. See text for abbreviations.

Systematic palaeontology

Saurischia Seeley, 1887
Sauropoda Marsh, 1878
Neosauropoda Bonaparte, 1996
Macronaria Wilson & Sereno, 1998
Camarasauromorpha Salgado *et al*., 1997
Genus ***Europasaurus*** Mateus, Laven, & Knötschke in Sander *et al*., 2006
Europasaurus holgeri Mateus, Laven, & Knötschke in Sander *et al.*, 2006
(Figs 1–28)

Holotype. DFMMh/FV 291, consisting of a disarticulated left premaxilla (DFMMh/FV 291.18), right maxilla (DFMMh/FV 291.17), right quadratojugal (DFMMh/FV 291.25), fragment of a braincase (DFMMh/FV 291.15), left laterosphenoid–orbitosphenoid complex (DFMMh/FV 291.16), right surangular (DFMMh/FV 291.10), left prearticular (DFMMh/FV 291.24), left dentary (DFMMh/FV 291.11), teeth (DFMMh/FV 291), cervical and sacral vertebrae, and cervical and dorsal ribs assigned to one individual.

A right angular, initially listed as part of the holotype (Sander *et al.* 2006) is excluded from this specimen, as the size of it is too small compared with the other mandible bones (Maprmann *et al.* 2011).

Referred material. The referred material represents at least 12 individuals, but probably several more. The minimum number of individuals was calculated based on the dentaries, including left and right elements of different sizes (Sander *et al.* 2006). Except for the holotype, a specimen composed of five sacral and 13 caudal vertebrae and chevrons (DFMMh/FV 100), and DFMMh/FV 838, which is composed of four middle to posterior cervical vertebrae, all preserved elements are regarded as different specimens, as neither obvious association nor articulation can be well established among them. See Online Supplementary Material for a complete list of the referred specimens.

Horizon and locality. Late Jurassic, middle Kimmeridgian marine carbonate rocks, bed 93 of section at Langenberg Quarry, Lower Saxony basin, Oker near Goslar, State of Lower Saxony, northern Germany.

Emended diagnosis. *Europasaurus holgeri* is diagnosed on the basis of the following characters, based on the holotype and referred specimens: (1) frontal with a very deep orbital rim causing an extreme reduction of the frontal–prefrontal and frontal–nasal articulations; (2) absence of quadratojugal–maxilla contact and large participation of the jugal to form the ventral margin of the skull (reversal to the condition observed in *Shunosaurus* and more basal sauropodomorphs); (3) presence of postparietal foramen (convergently acquired in some diplodocoids); (4) anterior cervical vertebrae without an anterior centrodiapophyseal lamina; (5) cervical vertebrae with well-developed prespinal and postspinal laminae (convergent with *Isisaurus*; Wilson & Upchurch 2003); (6) scapular acromion with a prominent posterior projection; and (7) transverse width of astragalus twice its dorsoventral height and anteroposterior length.

Comments. The presence of a marked notch in the cervical vertebrae was also regarded as an autapomorphic character of *Europasaurus* (Sander *et al*. 2006). However, the presence of an equally well-developed notch in the cervical vertebrae of *Giraffatitan* (MNH SII) and *Euhelopus* (PMU 233) indicates that this character is not an autapomorphy of *Europasaurus.* Up to now, this notch was not described or observed in other sauropods. For the moment, and due to its presence in relatively basal macronarian taxa, we prefer to exclude this character from the diagnosis of *Europasaurus*.

Description

The following description is mainly based on the most complete elements. The postcranial axial skeleton is divided into four major regions (i.e. cervical, dorsal, sacral and caudal). Vertebrae from these regions are further assigned to anterior, middle or posterior locations. Immature specimens were recognized as such primarily by their open or unfused neurocentral sutures. Open sutures commonly led to complete disarticulation, with only the centrum or the neural arch of a specific vertebra being represented. The immature specimens are described last in each section. Size itself is not a criterion for maturity, as has been well documented in *Europasaurus*, because the material of this genus comprises a small and a large morph; specifically, there are small mature vertebrae and large immature vertebrae. The meaning of this size dimorphism is discussed after the descriptions.

Cervical vertebrae

The cervical series is probably the best represented part of the *Europasaurus* postcranial axial skeleton, with elements that represent anterior, middle and posterior cervical vertebrae. These elements include mature vertebral elements as well as immature isolated centra and neural arches. Indeed, the cervical series provides the most valuable information about the morphological changes throughout the cervical series and ontogeny of this taxon.

As noted above, articulated and complete cervical series are not commonly preserved among Macronaria, making it difficult to estimate the total number of cervical vertebrae of *Europasaurus*. Among the few complete camarasauromorph necks are those of *Camarasaurus* (12 cervical vertebrae; Gilmore 1925), *Euhelopus* (16 cervical vertebrae; Wilson & Upchurch 2009), the unnamed titanosaur from Peirópolis, Brazil, known as 'Titanosauridae indet. DGM Series A' (13 cervical vertebrae; Powell 2003), and *Rapetosaurus* (17 cervical vertebrae; Curry Rogers 2009). Some common changes are observed through the neck of these taxa. As was noted by Gomani (2005), the interprezygapophyseal distance, the development of laminae and fossae on the lateral surface of the neural arches, and the length of the diapophyses increase posteriorly. Sauropod cervical vertebrae show a progressive increase in the elongation of the centra, from the second cervical element (the axis) to the middle cervical vertebrae (e.g. among ninth cervical vertebra in *Camarasaurus*; Osborn & Mook 1921). A progressive reduction of this elongation is observed from the middle cervical vertebrae to the dorsal vertebrae. Additionally, the cervical vertebrae of some sauropods (e.g. *Jobaria*, *Camarasaurus*; MNN TIG6;

Osborn & Mook 1921) display a continuous development of the paired CPOF, and the sTPOL. The paired CPOF appears in middle cervical elements of most neosauropods (sixth cervical vertebra in *Camarasaurus*, Osborn & Mook 1921; eighth cervical vertebra in *Apatosaurus*, Gilmore 1936) and is also present in more basal forms such as *Cetiosaurus* (Upchurch & Martin 2002). In these taxa, a large sTPOL first appears in anteroposterior cervical vertebrae and becomes more developed through the most posterior cervical elements. Although this pattern seems to be widespread among neosauropods, in *Giraffatitan brancai* (HMN-MB SI) the sTPOL and the CPOF are present and well developed in the third cervical vertebrae and decrease posteriorly.

Because many cervical elements of *Europasaurus* representing different ontogenetic stages were found in isolation and without association, some of the common changes observed in other sauropods must be considered carefully, especially because most of them can change through ontogeny or evolution. First, the relative length of the centra in sauropods seems to change drastically during ontogeny (e.g. Ikejiri 2004; Schwarz *et al.* 2007). Secondly, as was noted by Wedel (2003), the degree of pneumatization increases through ontogeny. Thirdly, the development of the sTPOL and CPOF seems to change during evolution (as revealed by the differences between *Camarasaurus* and *Brachiosaurus*).

Because of the aforementioned difficulties, the exact position of each isolated *Europasaurus* vertebra in the neck is difficult to determine with certainty. Nevertheless, when all of the morphological changes are taken into account, several major transformations through the cervical series can be detected. In *Europasaurus*, the development of the CPOF, its related laminae (mdCPOL) and the sTPOL show the same pattern observed in *Camarasaurus*, as is evident in the continuous sequence of four cervical vertebrae from a single specimen (DFMMh/FV 838; see below). The development of these fossae and laminae seems to change slightly through ontogeny, and because they are present even in early juvenile specimens (Carballido *et al.* 2012a), they can provide a good indicator of vertebral position.

As noted, for descriptive purposes the cervical vertebrae were divided into three sections as follows: anterior cervical vertebrae lack the CPOF; middle cervical vertebrae show weakly developed CPOFs; and posterior cervical vertebrae preserve well-developed CPOFs and sTPOL.

Atlas. Five atlas elements are preserved, which were identified as a complete (DFMMh/FV 910; Fig. 1A–C) and a fragmentary intercentrum (DFMMh/FV 204), and three complete or almost complete right neurapophyses (DFMMh/FV 362, 775, 791; Fig. 1D–I). The unfused nature of those elements is interpreted as a sign of immaturity; currently no mature atlas is known for *Europasaurus*.

The complete intercentrum is very small, being 21 mm wide with an anteroposterior length of 7.1 mm. In anterior and posterior views, the intercentrum is crescent shaped, and 1.6 times wider (21 mm) than high (13.4 mm; Fig. 1A, B). The dorsal concave region, which serves as support for the odontoid process of the axis, is not very deep (2.4 mm). Thus, the contacts for the neurapophyses do not project far dorsally and are short. The condiloid fossa is also crescentic, following the shape of the intercentrum, and occupies most of the anterior side of the intercentrum. The posterior side is only slightly convex (Fig. 1B). The anterior surface projects ventrally more than the posterior surface, a difference that is clearly visible in lateral view (Fig. 1C), but the anteroventral lip-like projection present in Flagellicaudata (Wilson 2002) and some titanosaurs (e.g. *Mongolosaurus*; Mannion 2011) is lacking. Despite the immature condition of the neurapophyses, some morphological differences were observed among them. The smallest of the atlas neurapophysis (DFMMh/FV 791; Fig. 1D–F) is more robust than the two larger elements (DFMMh/FV 362, 775; Fig.1G–I). As in other sauropods, the neurapophyses are wing-like structures directed posterodorsally. The ventral contact of the neurapophyses with the centrum is V–shaped in lateral view (Fig. 1F, H). The posterodorsal process of the neurapophysis, which gives support to the postzygapophysis, is further developed posteriorly in the largest than in the smallest element. Thus, when the anteroposterior lengths of the neurapophyses are compared with their heights, a shorter ratio in the smallest element is observed, giving this element a more robust aspect in lateral view (Fig. 1F, H). This difference is interpreted as resulting from the elongation in the atlas of *Europasaurus* through ontogeny, as described for the cervical vertebrae of other sauropods (e.g. Schwarz *et al.* 2007).

High and prominent epipophyses are present above the postzygapophyses of the largest neurapophyses. The epipophyses are separated from the postzygapophysis by a shallow lateral groove and are extended further posteriorly. The development of the epipophyses is higher in the larger neurapophysis, and becomes shorter in the smallest element, a difference that is also interpreted as an ontogenetic change in the shape of the atlas in *Europasaurus*. Two small foramina are posterodorsally located in the largest elements (Fig. 1I) but cannot be distinguished in the smallest neurapophysis.

Axis. Two complete neural arches are preserved (DFMMh/FV 563.2 and 706.1). Both neural arches show the characteristic zipper-like structure in their pedicels, indicating that they are immature elements. The smallest element (DFMMh/FV 563.2; Fig. 2A–C) is almost the half size of the largest one (DFMMh/FV 706.1; Fig. 2D–F). This difference in size is correlated with some differences observed in laminae and fossae development (i.e. PRDL, PODL and POCDF; Fig. 2) and is interpreted as different

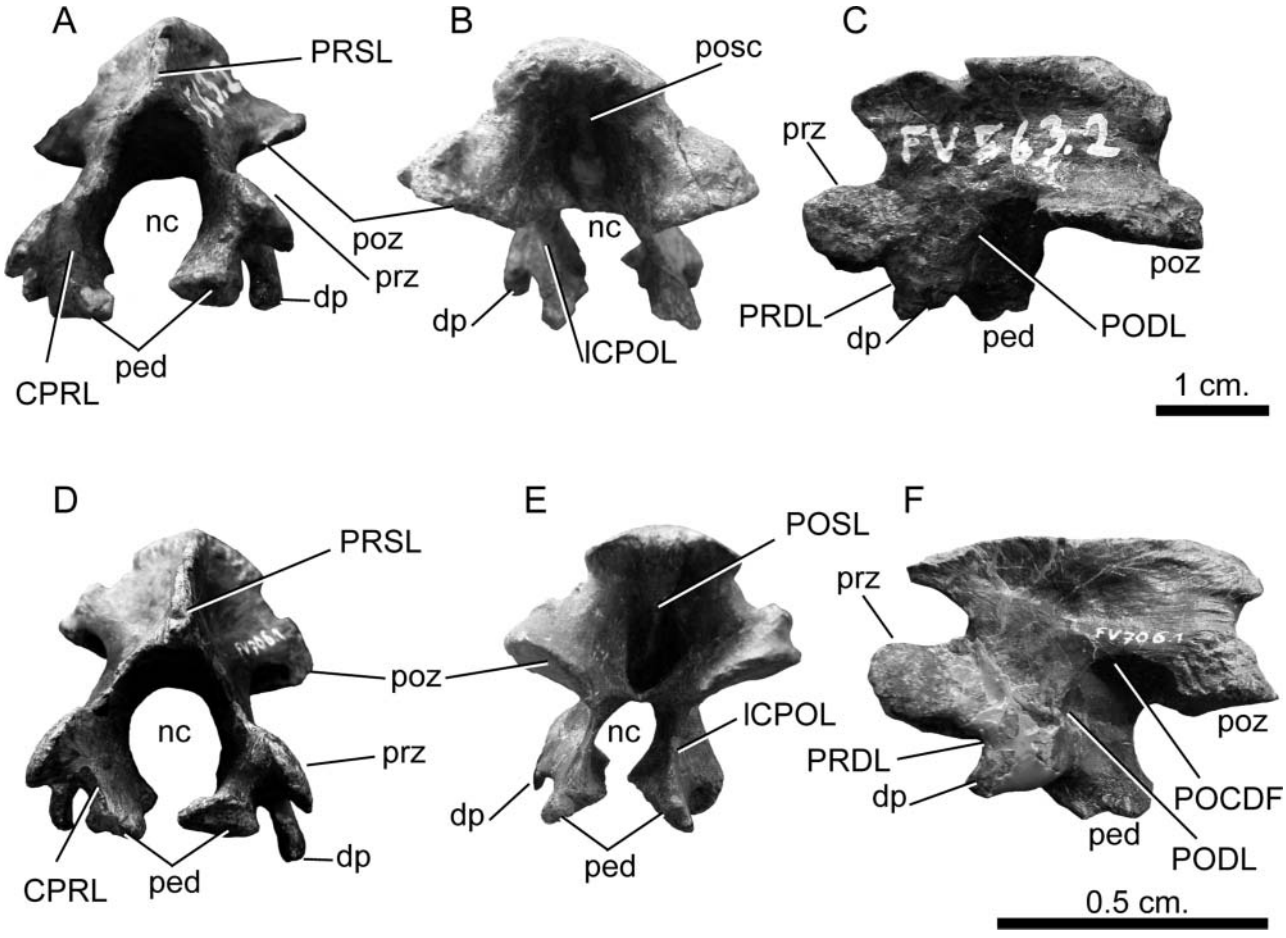

Figure 2. *Europasaurus holgeri*, axis. **A–C**, DFMMh/FV 563.2 in **A,** anterior, **B,** posterior and, **C,** lateral views. **D–F,** DFMMh/FV 706.1 in **D,** anterior, **E,** posterior and **F,** lateral views.. See text for abbreviations.

ontogenetic stages of those elements, with the smaller one being the more immature.

The transverse process is ventrally directed and ends in a thin and small diapophysis. This process is dorsally supported by the PODL and PRDL, which are well developed in the larger element and slightly developed in the smaller element (interpreted as the more immature one). Whereas in the larger neural arch, a well-developed and dorsally excavated POCDF is present below the PODL, in the smaller one this fossa is completely missing, indicating that the fossa was not present in the earliest stages. The prezygapophyses are highly inclined (around 70° with respect to the horizontal) and ventrally supported by a single CPRL. The prezygapophyses are positioned at mid-height on the neural canal. The neural spine is formed mainly by a single lamina, which is interpreted as the PRSL and can be observed well in anterior view (Fig. 2A, D). The PRSL posteriorly ends as a narrow lamina, which dorsally contacts the paired SPOL.

The postzygapophyses are less inclined than the prezygapophyses, showing an angle of no more than 30° with respect to the horizontal. From below, a thin and single lCPOL links the ventromedial end of the zygapophyses with the centrum. The paired TPOL runs anteromedially and forms the ventral edge of the SPOF. In both elements, but better developed in the larger one, a thin POSL is set into this fossa and runs dorsally. This single lamina is virtually absent in the smallest element, and only a small scar is discernible in this region (Fig. 2B), a change interpreted as a product of the earliest morphological ontogenetic stage of this element. Above the postzygapophysis, a moderately developed epipophysis is present, which is not as high or posteriorly developed as in the neurapophyses of the atlas. A robust SPOL runs from the postzygapophysis up to the dorsal end of the neural spine (Fig. 2B, E).

Mature anterior cervical vertebrae. A total of 11 anterior cervical elements were identified. The four more complete vertebrae have several differences in their laminae and fossae, which are interpreted as indicative of different positions in the anterior section of the neck, and also different ontogenetic stages (see below). Element DFMMh/FV

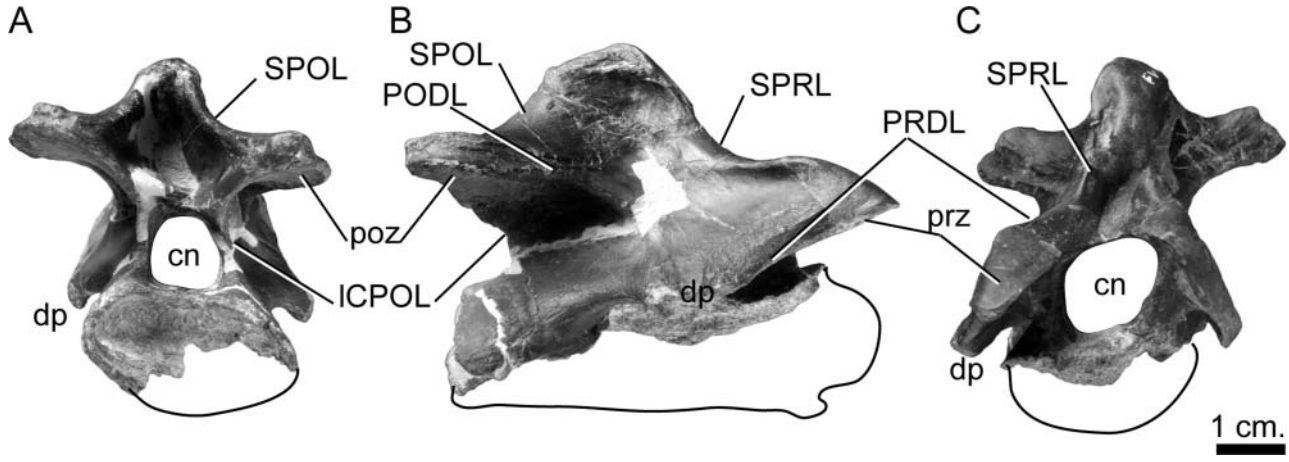

Figure 3. *Europasaurus holgeri*, anterior cervical vertebra (DFMMh/FV 999.1; third?) in **A,** posterior **B,** lateral and **C,** anterior views. See text for abbreviations.

999.1 (Fig. 3) is considered to be the anteriormost cervical vertebra preserved in *Europasaurus* (excluding the atlas–axis), being probably the first one after the axis, a position hypothesized based on the absence of some laminae and the weak development of fossae. Another element (DFMMh/FV 652.1; Fig. 4) is also assigned to an anterior position, but not as anterior as DFMMh/FV 999.1; it probably represents the fourth cervical vertebra of *Europasaurus*. The anterior position of this element is indicated by its relatively shorter centrum as well as other morphological characteristics, such as the low diapophysis and the short lCPOL. The other preserved vertebrae are relatively longer (Online Supplementary Material; Fig. 5), being assigned to a more posterior position in the anterior section of the neck. Additionally, several other morphological changes (e.g. shape of the pleurocoel and orientation of the laminae) support a more posterior position for these elements (see below).

The centra are opisthocoelous with a distinctive notch in the dorsal edge of the posterior articular surface, just below the neural canal. This medial notch is especially visible in dorsal view (Figs 4B, 5C, D) and has been described as an autapomorphic character of *Europasaurus* (Sander *et al*. 2006). Nevertheless, its presence in *Giraffatitan brancai* (HMN-MB SII) and *Euhelopus* (PMU 233) indicates that this character is present in other camarasauromorph sauropods, and thus we excluded it from the diagnosis of *Europasaurus* (see above) and included it as a new character in the phylogenetic analysis. This medial notch is especially well developed in mature specimens (DFMMh/FV 999.1, 652.1 and 291.4), but is extremely reduced or absent in immature elements. The plane of the posterior articular surface of the centra is slightly anterodorsally inclined rather than perpendicular to the axes of the vertebra. Ventrally, the centra are transversely flat at midlength but, resulting from the ventral orientation of the parapophyses, they are slightly concave at the parapophysis level. Only one of the elements shows a deep concave region at parapophysis level (DFMMh/FV 46), but this seems to be the result of the mediolateral diagenetic compression. No ventral keels or anteroposteriorly oriented ventral cavities are present in any of the preserved cervical elements. The parapophysis process is ventrolaterally oriented from the centrum, and the capitular articulation is anterolaterally directed (Fig. 4).

The centra are laterally excavated, but differences in the degree of pneumatization are observed among different elements. These differences are interpreted as resulting from the ontogenetic stage, as well from the relative position in the anterior section of the neck. In specimens DFMMh/FV 291.4 and 652.1, the centra are most deeply excavated, leaving only a very small septum, which separates the left and right pleurocoels (Figs 4C, 5B). In these two elements, the excavation of the pleurocoel extends into the centrum in all directions. The other two vertebrae (DFMMh/FV 46 and 701.1) are laterally excavated, but their pleurocoels do not open as deeply into the centra, especially in their posterior half.

The probable fourth cervical vertebra (DFMMh/FV 652.1) shows a deep pleurocoel divided by a thin septum oriented anterodorsally (Fig. 4C). This division is also present in the other mature and well-excavated element (DFMMh/FV 291.4; Fig. 5B), but is less developed than in the former. A similar development of this ridge is present in the two less mature elements, at least on one of their sides (as they are asymmetrically excavated). Because these elements were interpreted as having a posterior position among the anterior cervical vertebrae, a well-divided pleurocoel seems to only occur in the anteriormost cervicals of *Europasaurus*. Although no complete cervical series is preserved, the presence of a weak ridge in the posterior anterior cervical vertebrae, and its absence in middle

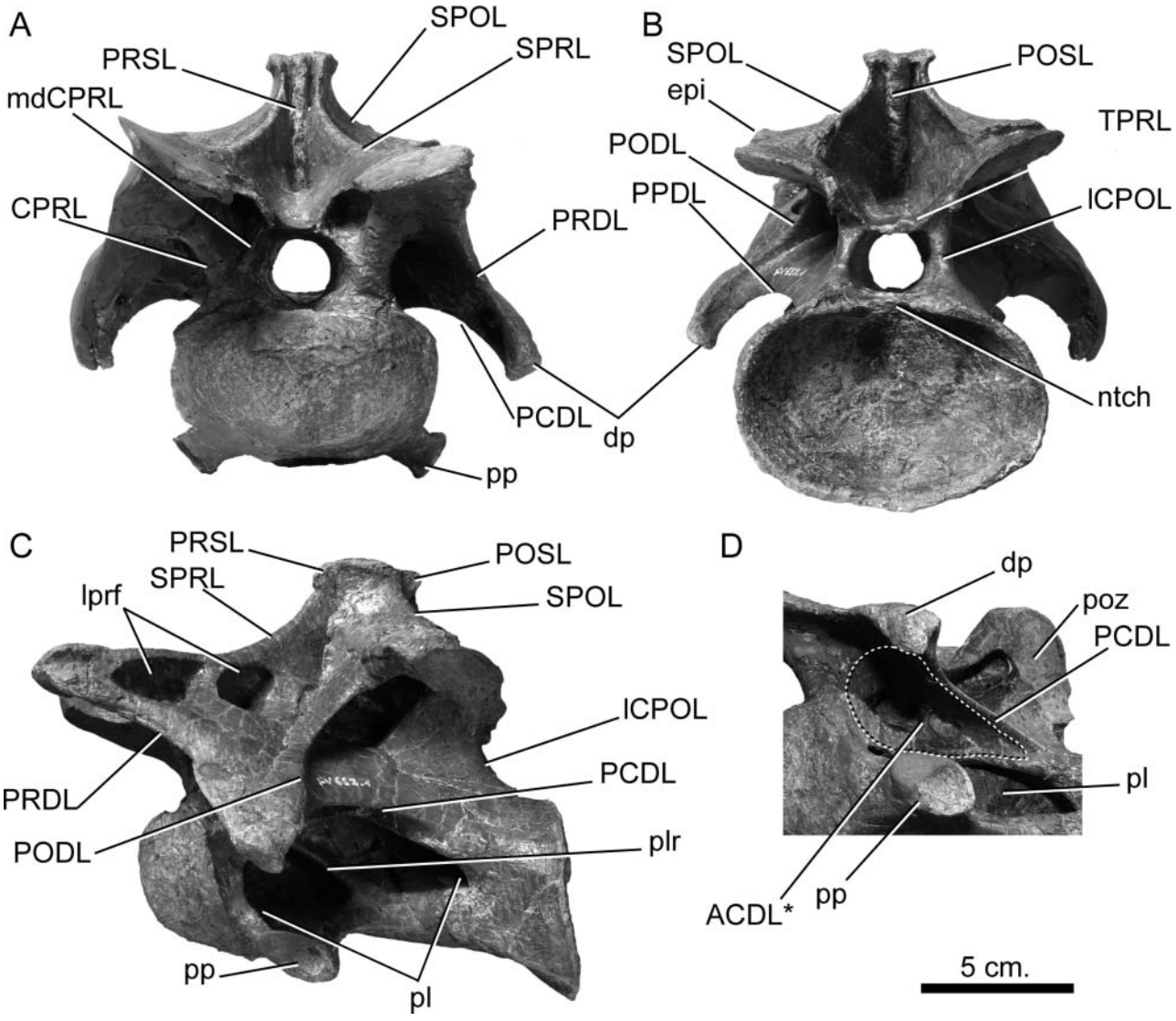

Figure 4. *Europasaurus holgeri*, anterior cervical vertebra (DFMMh/FV 652.1) in **A,** anterior, **B,** posterior, **C,** lateral and **D,** anteroventral views. See text for abbreviations.

and posterior cervical elements (see below), indicate that this division gradually disappears posteriorly in anterior cervical vertebrae. Therefore, the morphology of *Europasaurus* cervical vertebrae resembles the condition of *Camarasaurus* instead of the more complex pleurocoel of brachiosaurids such as *Giraffatitan*. The parapophysis is dorsally excavated, and this small excavation is continuous with the pleurocoel of the centra, resembling the condition of some basal sauropods and *Camarasaurus* (Upchurch *et al.* 2004).

The transverse process is ventrally supported by a well-developed PCDL. This lamina is anterodorsally oriented, laterally projected and runs from the posterior end of the pleurocoel to reach the diapophysis from the posteroventral margin of the transverse process (Figs 3–5). As is typical for the cervical vertebrae, the transverse process is ventrally inclined with its diapophysis anteroventrally directed (Figs 3–5). A deep CDF is present and heavily penetrates the neural arch in all the anterior cervical vertebrae (Fig. 4D). A midline ridge, dorsoventrally oriented, which slightly divides the CDF, is present in the anterior cervical vertebrae except in the anteriormost cervical element DFMMh/FV 999.1. Although this ridge could be interpreted as an early stage of the ACDL, its persistence in more posterior cervical elements, in which the 'true' ACDL first appears (see below), indicates that this ridge is a different lamina. Therefore, it is advisable to use a different name, referring it as the ACDL* (Fig. 4D) to denote its similarities with the 'true' ACDL. Due to the absence of the ACDL in anterior cervical vertebrae of *Europasaurus*, no PRCDF

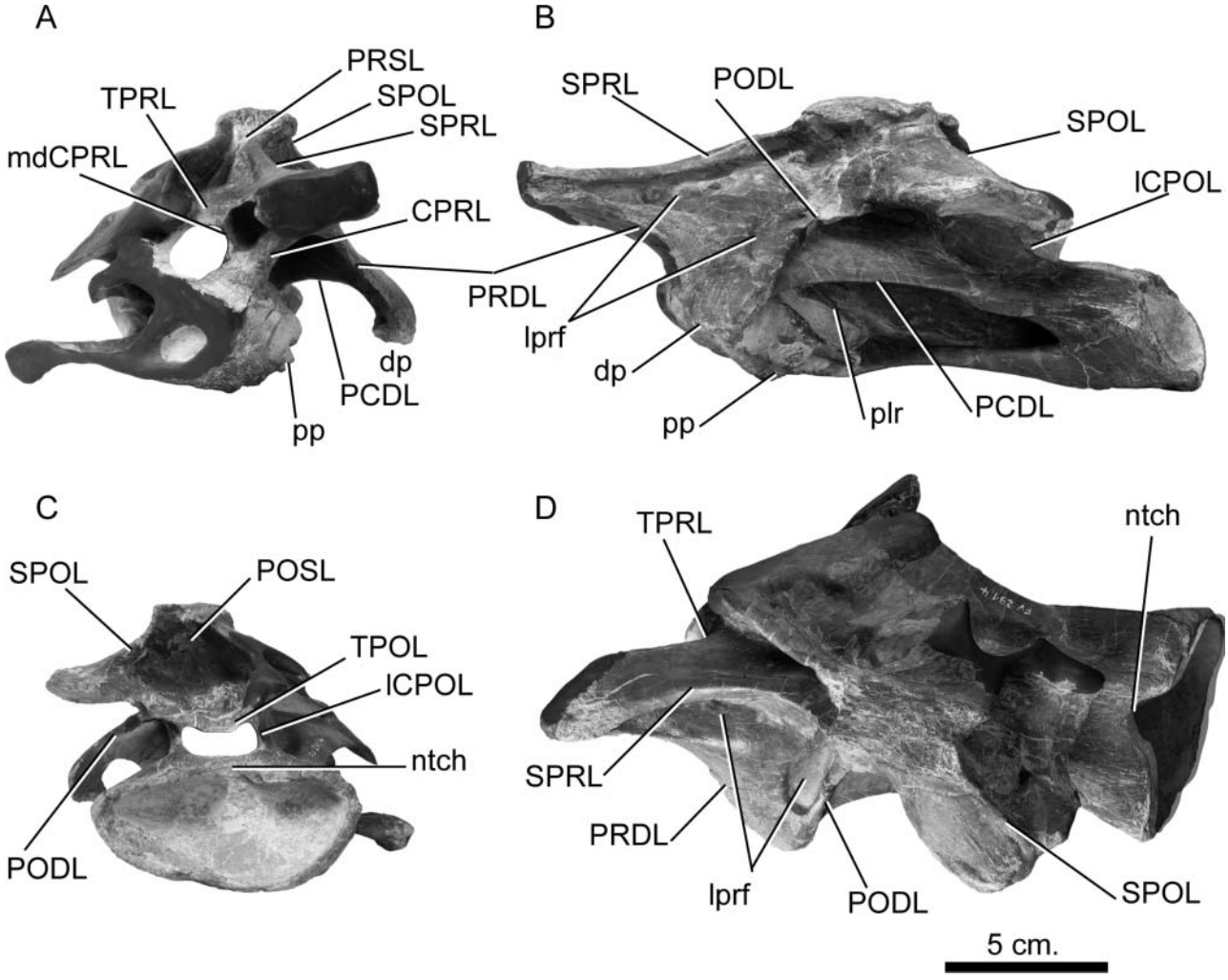

Figure 5. *Europasaurus holgeri*, anterior cervical vertebra (DFMMh/FV 291.4) in **A,** anterior, **B,** lateral, **C,** posterior and **D,** dorsal views. See text for abbreviations.

can be recognized. The absence of the ACDL in anterior cervical vertebrae, and thus the presence of only a single fossa below the diapophysis, is a unique character among basal macronarians, and thus represents an autapomorphic character of *Europasaurus*.

Dorsally, two laminae link the transverse process with the prezygapophysis and the postzygapophysis. These laminae are, respectively, the PRDL and the PODL. The PRDL runs from the anterodorsal part of the diapophysis to the lateroventral part of the prezygapophyses, projecting ventrolaterally (Figs 3B, 4A, C, 5A, B). The second lamina, the PODL, runs from the posterodorsal edge of the transverse process, reaching the level of the diapophyses, to the anteroventral part of the postzygapophysis (Figs 3B, 4B, C, 5B, C). This lamina is posterodorsally oriented, delimiting the dorsal edge of the POCDF. The fossa is present and well developed in all the anterior cervicals but is smallest in the anteriormost cervical vertebra (Fig. 3).

The prezygapophyses are flat and ventromedially inclined, forming an angle of around 20° with respect to the horizontal (Fig. 4A). In anterior view, a triangular and well-delimited paired CPRF is present below the prezygapophysis (Figs 4A, 5A). The CPRL is divided at mid-height, just above the neural canal, resulting in a narrow medial division of the CPRL (mdCPRL). The mdCPRL extends dorsomedially, from the stout CPRL up to the medioventral edge of the TPRL, just above the neural canal. The mdCPRL is present in all of the anterior cervical vertebrae except for the axis and the anteriormost preserved cervical element (DFMMh/FV 999.1), in which a single CPRL is observed (Fig. 3A). The presence of mdCPRL is a widespread character among non-titanosaur macronarians (e.g. *Bellusaurus*, IVPP V8299; *Giraffatitan*, HMN-MB SII; *Paluxisaurus*, Rose 2007). The prezygapophyseal process laterally exhibits one or two well-developed lateral fossae, similar to those present in *Giraffatitan* (Janensch 1950).

In posterior view, a short and dorsally directed lCPOL links the centrum with the ventromedial margin of the postzygapophysis. This paired lamina is dorsally expanded (Figs 3A, 4C, 5C), but without any signs of fossae or cavities, and thus differing from the morphology of the middle and posterior cervical vertebrae. Both postzygapophyses are connected to each other by the paired TPOL. The TPOL bounds the flat dorsal margin of the neural canal. The postzygapophyses are dorsally directed in the ventral part, and then abruptly turn laterally (Fig. 4B).

The neural spine of the anterior cervical vertebrae is undivided and short. In the anteriormost preserved anterior cervical vertebrae (DFMMh/FV 999.1 and 652.1), the neural spine is almost as long as wide, whereas it is around 1.5 times longer in DFMMh/FV 291.4, and two times longer in DFMMh/FV 701.1. This difference is interpreted as a morphological change in the shape of the neural spine through the anteriormost cervical vertebrae. The two paired laminae of the neural spine, SPRL and SPOL, are highly developed (Figs 3–5). The single laminae, PRSL and POSL, are well developed and have a rough aspect throughout their length. Anteriorly, the SPRL arises on the dorsolateral aspect of the prezygapophysis, and runs dorsomedially up to two thirds of the neural spine height. At this height, both SPRLs (left and right) become parallel and dorsally oriented (Fig. 4A, C), bounding the SPRF, within the PRSL. In posterior view, the SPOL runs dorsomedially from the dorsolateral aspect of the postzygapophysis to near the end of the neural spine. At this height, the SPOLs become parallel to each other and are dorsally oriented (Fig. 4B, C), taking a similar shape to the one observed in the anterior edge of the neural spine. A triangular and deep fossa, the SPOF, is present above the postzygapophysis. This fossa is bounded ventrolaterally by the TPOL and dorsolaterally by the SPOL. The single POSL is enclosed in this fossa and runs posterodorsally, from the deepest part of the SPOF up to the dorsal tip of the neural spine (Figs 4B, C, 5C).

Immature anterior cervical neural arches. The general morphology of the largest preserved immature element (DFMMh/FV 857.3; Fig. 6A–C) does not differ significantly from the mature neural arches described above, and therefore is interpreted as showing an advanced immature stage. In contrast, the three smallest immature neural arches (DFMMh/FV 119, 833.1 and 1031) show several morphological differences. Although size by itself cannot be used as a direct indicator of maturity (Brochu 1996), the very small size of these neural arches suggests that they came from very young individuals, which is also congruent with the morphological differences observed between them and mature elements. Moreover, these three small neural arches show some differences, which can be used to infer different ontogenetic stages, with DFMMh/FV 119 being slightly more developed than the other two.

The CDF of DFMMh/FV 119 is present and well developed, whereas the POCDF is also present but is not as deep as in mature elements or in DFMMh/FV 857.3 (Fig. 6A–C). Although the POCDF can be regarded as present, it is not as developed as in mature elements (see above; Figs 4, 5) or in the advanced immature vertebrae (DFMMh/FV 857.3; Fig. 6A–C). Prespinal and postspinal laminae are virtually absent, and only a slightly marked and rough scar is visible in these positions (Fig. 6D–F). These scars are not developed enough to be considered laminae but are interpreted as an early formation stage of laminae, and thus are referred to as the prespinal and postspinal scars (prsc and posc; Fig. 6D–N.

The other two neural arches (DFMMh/FV 1031 and 833.1) are interpreted as showing an earlier ontogenetic stage than DFMMh/FV 119. The few differences observed among them are related to their slightly different positions. DFMMh/FV 833.1 (Fig. 6J–N) is interpreted as one of the first cervical vertebrae, probably the third. This position is inferred because of the absence of the mdCPRL, which is present in all other anterior cervical vertebrae except for the anteriormost post-axial elements (see above and Fig. 3). Although the absence of this lamina could be interpreted as a result of a different ontogenetic stage, its presence in DFMMh/FV 1031 argues against this interpretation. Moreover, this lamina was recently described in an early juvenile sauropod individual (SMA 0009) from the Morrison Formation interpreted as a taxon closely related to *Brachiosaurus* (Carballido *et al.* 2012a).

In DFMMh/FV 833.1, the CDF and POCDF are slightly developed, and the lateral surface of the prezygapophyseal process does not show any lateral excavation. These morphological differences with respect to DFMMh/FV 1031 are interpreted as resulting from the anterior position of DFMMh/FV 833.1 and not as ontogenetic differences, as the same morphology is present in the anteriormost preserved post-axial cervical vertebra (DFMMh/FV 999.1; see above). In contrast, DFMMh/FV 1031 (Fig. 6G–I) has a well-developed mdCPRL and a weakly developed lamina below the diapophysis (which probably represents the ACDL*). The presence of these laminae is interpreted as resulting from a more posterior position. Although broken distally, the prezygapophyseal process of DFMMh/FV 1031 does not show any signs of lateral excavations, which are present in all cervical vertebrae except for the anteriormost elements. Because this neural arch is interpreted as having a posterior location among the anterior cervical vertebrae, the absence of excavations in the prezygapophyseal process is interpreted as resulting from the very early ontogenetic stage of this element. The neural spine of DFMMh/FV 1031 is completely preserved, being short and without the POSL, the PRSL or the prespinal scar. The SPRL and SPOL are present but these laminae are only slightly developed as narrow and low crests.

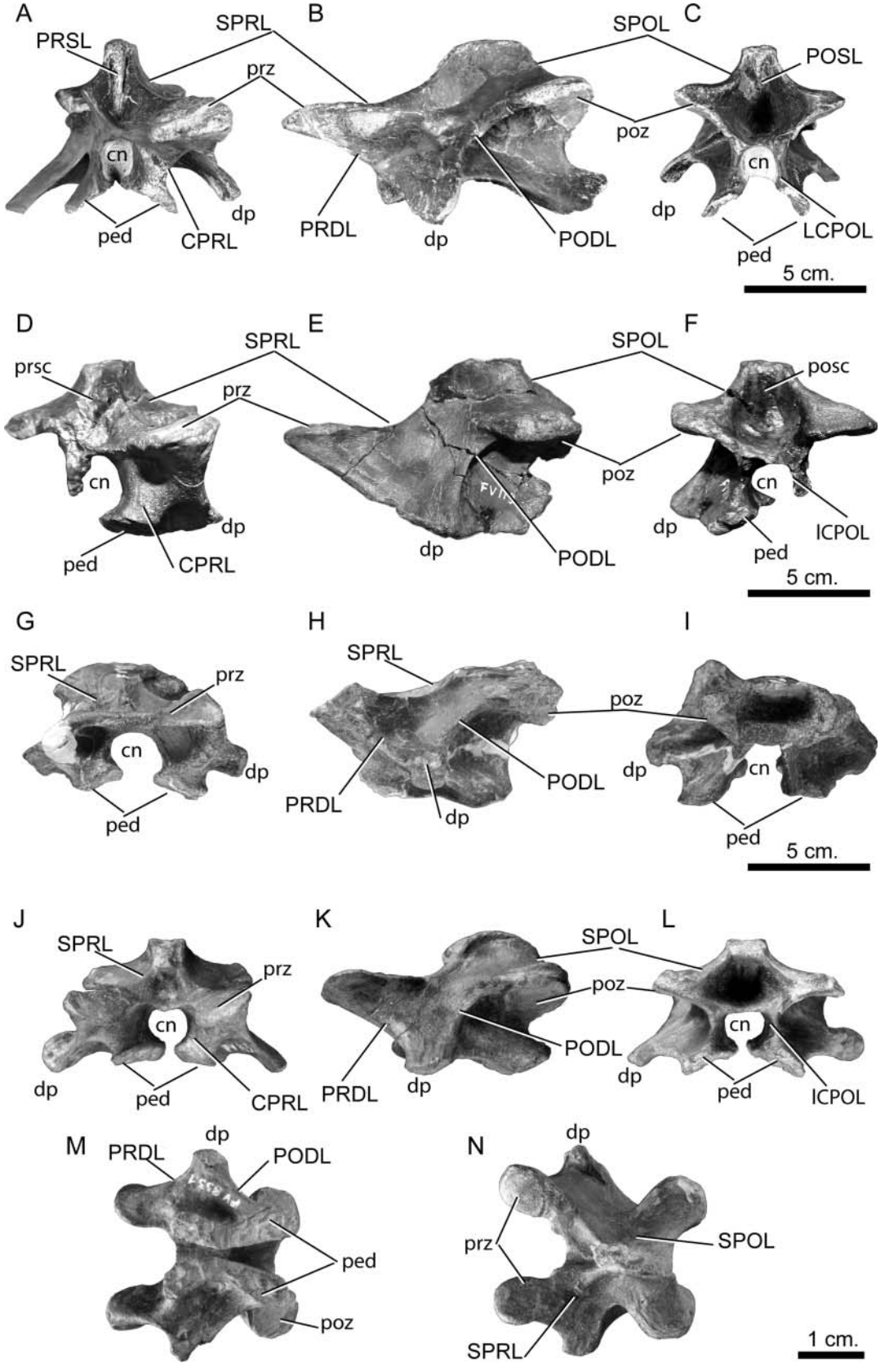

Figure 6. *Europasaurus holgeri*, immature anterior cervical vertebra. **A–C,** DFMMh/FV 857.3 in **A,** anterior, **B,** lateral and **C,** posterior views. **D–F,** DFMMh/FV 119 in **D,** anterior, **E,** lateral and **F,** posterior views. **G–I,** DFMMh/FV 1031 in **G,** anterior, **H,** lateral and **I,** posterior views. **J–N,** DFMMh/FV 833.1 in **J,** anterior, **K,** lateral, **L,** posterior, **M,** ventral and **N,** dorsal views. See text for abbreviations.

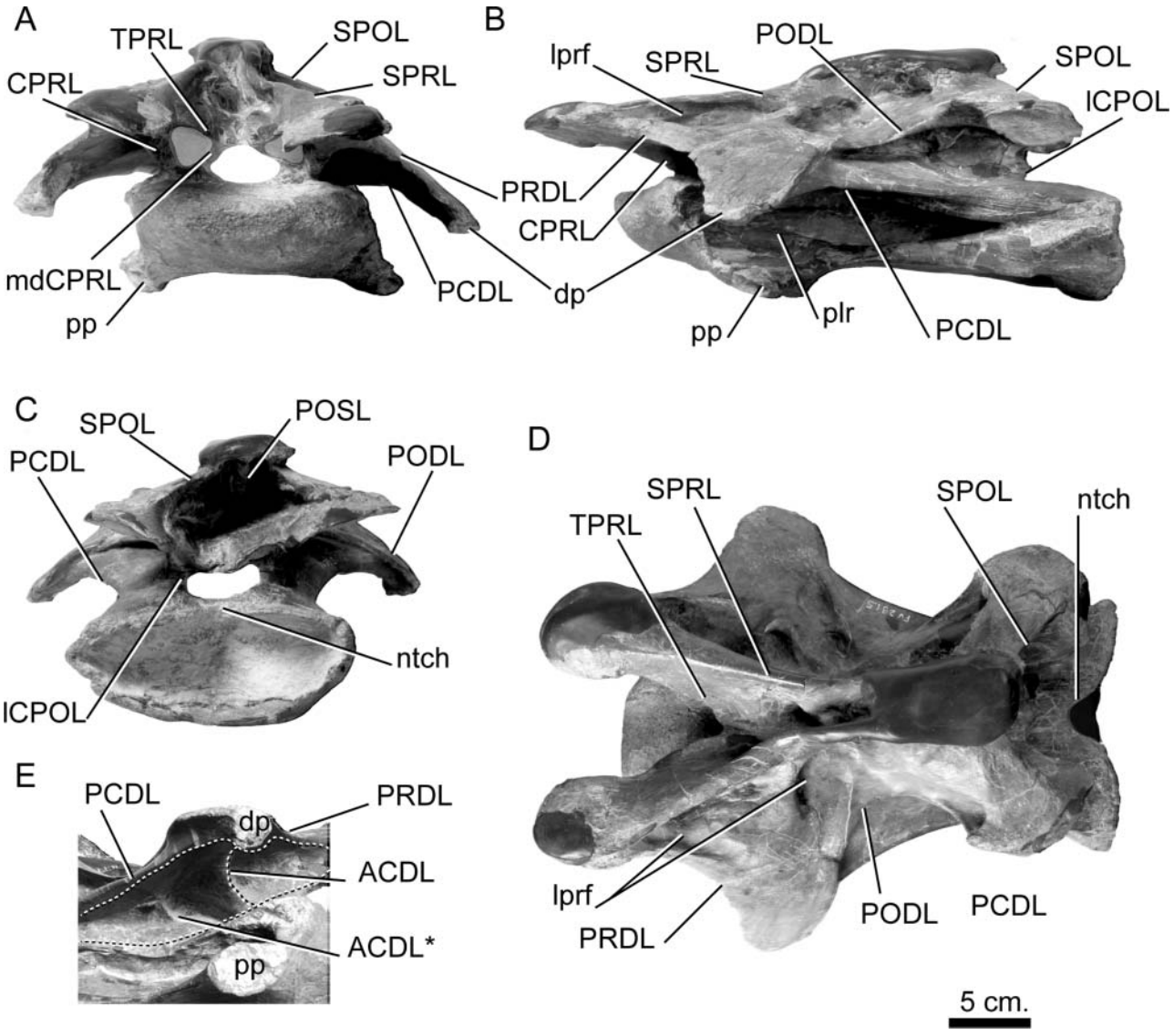

Figure 7. *Europasaurus holgeri*, mature anterior–middle cervical vertebra (DFMMh/FV 291.5) in **A,** anterior, **B,** lateral, **C,** posterior, **D,** dorsal and **E,** anteroventral views. See text for abbreviations.

Middle cervical vertebrae. A total of four mature middle cervical vertebrae are preserved. Whereas two of the vertebrae (DFMMh/FV 291.5 and 710) were found in isolation, the other two are part of a single individual composed of two middle and two posterior cervical vertebrae (DFMMh/FV 838; Figs 9, 12). In these middle cervical vertebrae, some morphological and size differences are observed (see Online Supplementary Material for measurements). The CPOF is present in all elements but is less developed in DFMMh/FV 291.5 and 710 (Figs 7C, 8C), and most developed in DFMMh/FV 838.11a, b (Fig. 9C, D), interpreted here as resulting from the more posterior position of the two latter elements. Therefore, the middle cervical vertebrae can be divided into anterior middle cervicals (DFMMh/FV 710 and 291.5) and posterior middle cervicals (DFMMh/FV 838.11a, b). All of the anterior cervical vertebrae show a similar ontogenetic stage, as their general morphology, laminae and fossae development do not greatly differ. Two different size classes are observed among these elements, independently of their slightly different positions. The smallest element (DFMMh/FV 710) is around half the size of the largest vertebrae (DFMMh/FV 291.5 and 838) (Online Supplementary Material).

The opisthocoelous centra have a well-developed notch on the dorsal surface of their posterior side (Figs 7D, 8C, 9C, D). In the middle cervical vertebrae this notch is better developed than in the anterior cervical vertebrae, indicating an increasing expression of the notch towards the middle cervical vertebrae. The plane of the posterior articular surface is inclined only slightly

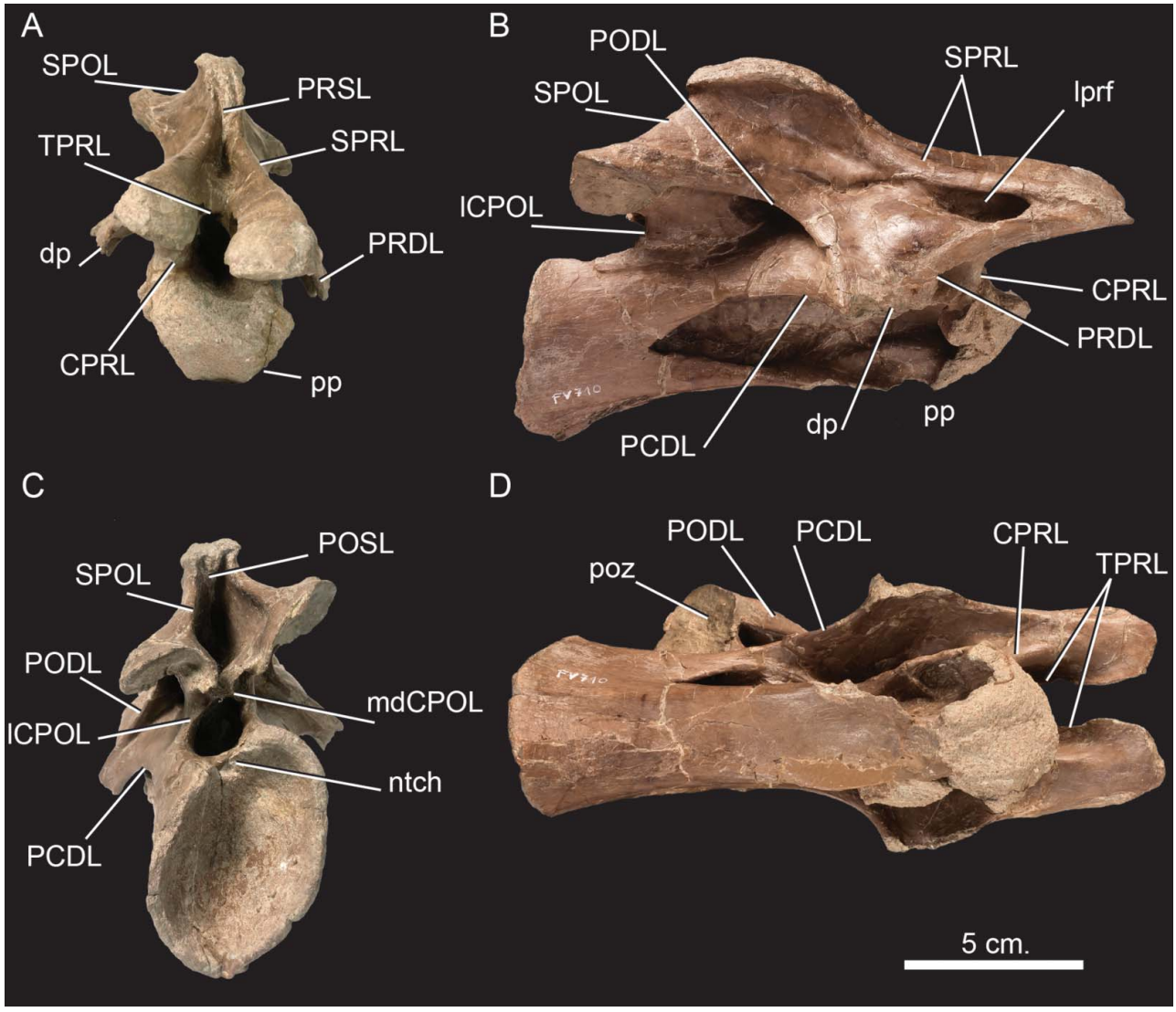

Figure 8. *Europasaurus holgeri*, mature anterior–middle cervical vertebra (DFMMh/FV 710) in **A,** anterior, **B,** lateral, **C,** posterior and **D,** ventral views. See text for abbreviations.

anterodorsally. In transverse section, the ventral surface of the centra is flat except for a shallow concavity at the level of the parapophysis (Figs 8B, 9B). As in anterior cervical vertebrae, the parapophysis is ventrally positioned, with the capitular articulation oriented anterolaterally. The ventral aspect of the middle cervical vertebrae does not differ from the morphology described for anterior cervicals.

Large posteriorly acute pleurocoels occupy most of the lateral aspect of the centra. The pleurocoels deeply excavate the centra, leaving only a thin septum in the midline of the vertebra. In contrast to the anterior cervical vertebrae, the pleurocoels are not divided by any kind of lamina or ridge and are therefore regarded as simple in their morphology. The CDF is well developed but is deeper than in the anterior cervicals. The PCDL runs from the posterior end of the pleurocoel toward the transverse process and reaches the posteroventral aspect of the diapophysis (Fig 7B, 8B, 9A). The ACDL* can be recognized in the entire middle cervical vertebra as a poorly developed lamina, which is even less developed in posterior middle cervical vertebrae (DFMMh/FV 51, 838.11a, b; Fig. 7E). A new lamina, not present in the anterior cervical vertebrae, is present in the middle cervicals. This new lamina, which is more anteriorly placed than the ACDL*, can be followed towards the posterior cervical and dorsal vertebrae, and is interpreted as the true ACDL (Fig. 7E). The ACDL becomes more developed towards the posteriormost middle cervicals and runs posterodorsally from near the ventral beginning of the CPRL down to the ventral aspect of the transverse process.

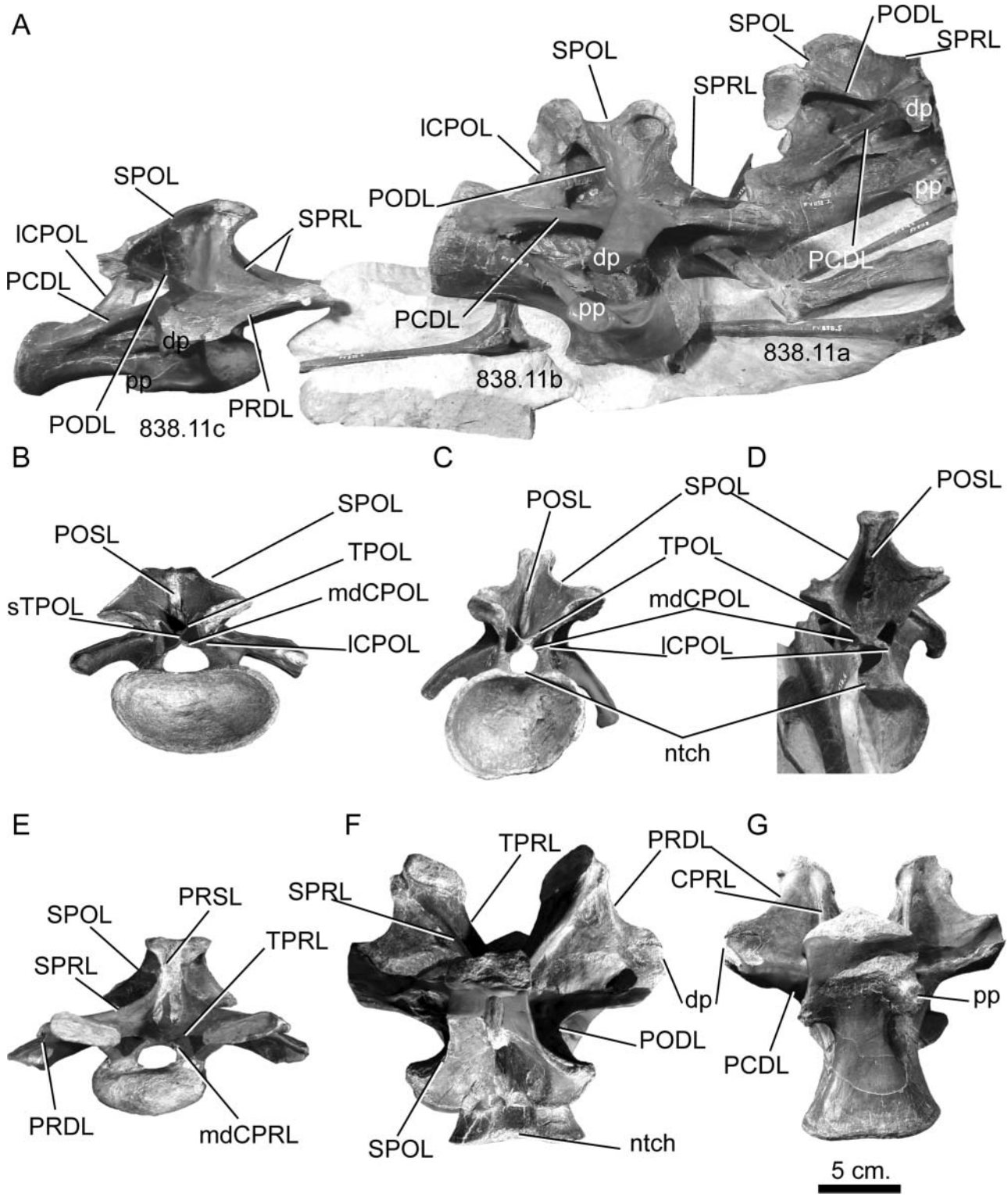

Figure 9. *Europasaurus holgeri*, mature posterior middle and anteroposterior cervical vertebrae. **A,** DFMMh/FV 838 series, lateral view. **B, E–G,** DFMMh/FV 838.11c in **B,** posterior, **E,** anterior, **F,** dorsal and **G,** ventral views. **C,** DFMMh/FV 838.11b in posterior view. **D,** DFMMh/FV 838.11a in posterior view. See text for abbreviations.

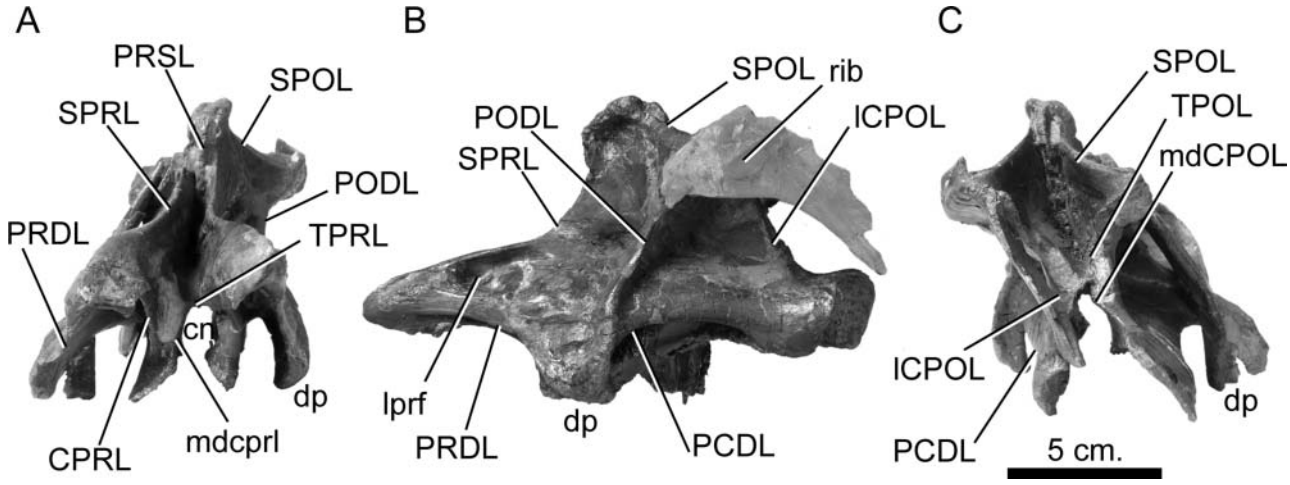

Figure 10. *Europasaurus holgeri*, immature posterior–middle cervical vertebra (DFMMh/FV 51) in **A,** anterior, **B,** lateral and **C,** posterior views. See text for abbreviations.

The co-occurrence of both laminae in the middle cervical vertebrae allows recognition of the two laminae below the diapophysis as the ACDL and the ACDL*, as noted for the anterior cervical vertebrae. The presence of a well-developed ACDL provides the origin for a new fossa not present in the anterior cervical vertebrae, the PRCDF. The PRCDF is only weakly developed in the anterior middle cervical vertebrae but becomes larger toward the posterior. The PRDL and PODL have the same morphology described for anterior cervicals, although with a slightly different inclination, as the diapophysis is higher than in anterior cervical vertebrae.

The prezygapophyses and its related laminae do not greatly differ from the morphology described for anterior cervical vertebrae (Fig. 7A) but the zygapophyses of the posterior middle cervical vertebrae have an angle of some 45°. The lCPOL remains relatively short in the anterior middle cervical vertebrae but becomes longer in the posterior middle cervicals (Fig. 9C, D). A triangular and paired CPOF is present below the postzygapophysis, giving rise to the mdCPOL (Figs 7C, 8C, 9C, D). This fossa is ventromedially bordered by the mdCPOL, laterally by the lCPOL, and dorsomedially by the TPOL. The CPOF of posterior middle cervicals is triangular-shaped. The TPOL is ventromedially oriented and is not as flat as in the anterior cervicals. In the middle cervicals, the ventrally inclined paired TPOLs converge on each other near the medial aspect of the neural arch and form a flat and short horizontal lamina (Figs 7C, 8C, 9C, D). This short contact among the TPOLs gives to the neural arch an acute dorsal end, which becomes even more notable in posterior cervical vertebrae in which the sTPOL is developed (see below).

The neural spine is about two times longer than wide in the anterior middle cervical vertebrae, and 1.5 times longer than wide in the posterior middle neural arches. The SPRL is dorsomedially oriented for most of its length. Near its dorsal end, the SPRLs are directed dorsally, being almost vertical in the posterior middle cervical vertebrae and running parallel to each other (Figs 7A, 8A). The rough and long PRSL extends between the two SPRLs, being set into the SPRF, as in the anterior cervical vertebrae. The lateral face of the neural spine is well excavated with one or more deep lateral fossae (Figs 7–9). As is the case for the PRSL, the POSL is well developed, but both laminae are slightly more developed in the more posterior middle cervicals.

Immature middle cervical neural arch. Only one neural arch (DFMMh/FV 51; Fig. 10) is preserved for this section of the neck. The size of this neural arch is comparable to the smallest mature middle cervical vertebra (DFMMh/FV 710). The general shape and the development of laminae and fossae do not greatly differ from morphologically mature vertebrae, and therefore DFMMh/FV 51 is regarded as an advanced immature element. The presence of a well-developed CPOF and its associated laminae (lCPOL and mdCPOL) allows the identification of this neural arch as a posterior middle cervical one. The main difference of DFMMh/FV 51 compared to more mature elements is the state of development of the pneumaticity; unlike mature elements. DFMMh/FV 51 is only slightly excavated (Fig. 10).

Immature anterior or middle cervical centra. Several isolated centra are preserved and identified as pertaining to either anterior or middle cervical vertebrae. These centra show the same general morphology observed in mature vertebrae. Although some are incomplete, they provide information on ontogenetic changes and also reveal the presence of two size classes among the material assigned to

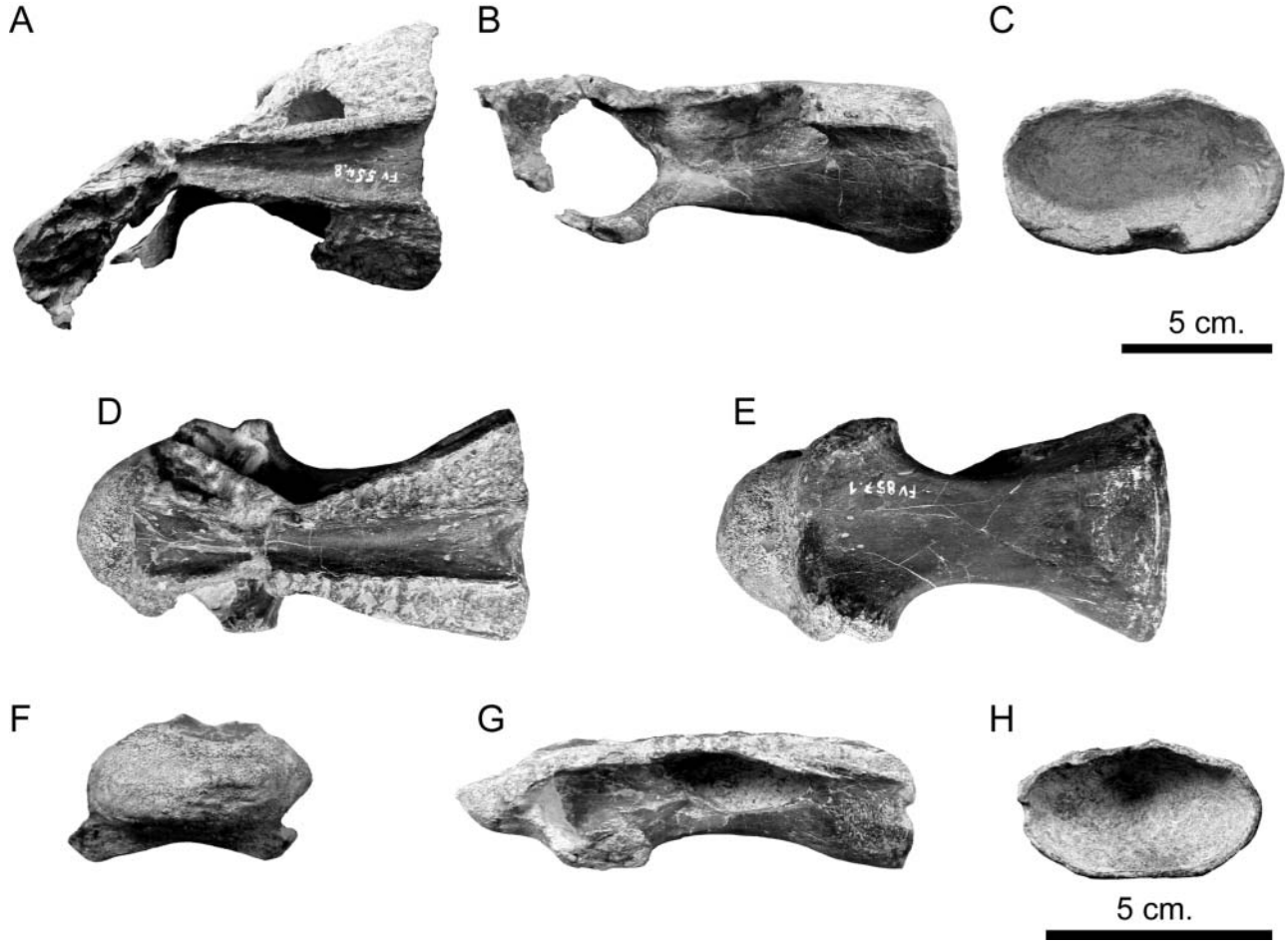

Figure 11. *Europasaurus holgeri*, immature anterior–middle cervical centra. **A–C,** DFMMh/FV 554.8 in **A,** dorsal, **B,** lateral and **C,** posterior views. **D–H,** DFMMh/FV 857.1 in **D,** dorsal, **E,** ventral, **F,** anterior, **G,** lateral and **H,** posterior views. See text for abbreviations.

Europasaurus. This difference in size was previously noted for the anterior and middle cervical vertebrae as well.

Preserved centra can be clearly grouped into small (DFMMh/FV, 51, 126, 783, 836.2, 857.1; Fig. 11D–H) and large (DFMMh/FV 785.1 and 554.8; Fig. 11A–C) (Online Supplementary Material). Whereas a small size is expected for such immature elements, the largest immature centra are comparable in size to the largest mature cervical vertebrae known for *Europasaurus* (DFMMh/FV 291.5 and series 838). They are therefore about twice as large as some of the mature elements described above (e.g. DFMMh/FV 710, 783; Online Supplementary Material). Such size differences are interpreted as evidence of two well-differentiated size classes among the elements and were also observed in the complete and mature elements from a similar ontogenetic stage described above (e.g. 701.1 is around the half size of 838.11 and 291.5, but has a similar position). In addition to different sizes, some morphological changes can be observed among the immature centra that are related to different ontogenetic stages of the immature specimens.

A well-developed notch in the dorsal margin of the posterior articular surface is present in the mature elements (see above). In all of the immature centra, even in the largest, the notch is absent or only slightly developed. As was previously noted, the expression of this notch changes along the cervical series, but the notch is always well developed in mature middle cervical vertebrae. The absence of the notch in the isolated middle cervical centra (e.g. DFMMh/FV 857.1; Fig. 11D) indicates that it becomes deeper during ontogeny.

As with the development of the notch, the depth of the pleurocoels also shows some differences among the centra. In all of the immature centra, the lateral surface of the pleurocoels is extremely vascularized. In all small immature specimens, the pleurocoels are only developed as shallow excavations on the lateral side of the centra. In these more immature elements the pleurocoels are well excavated anteriorly but become shallow posteriorly, lacking a distinct edge. The pleurocoels of the largest immature cervical centra are better developed, being similar in shape

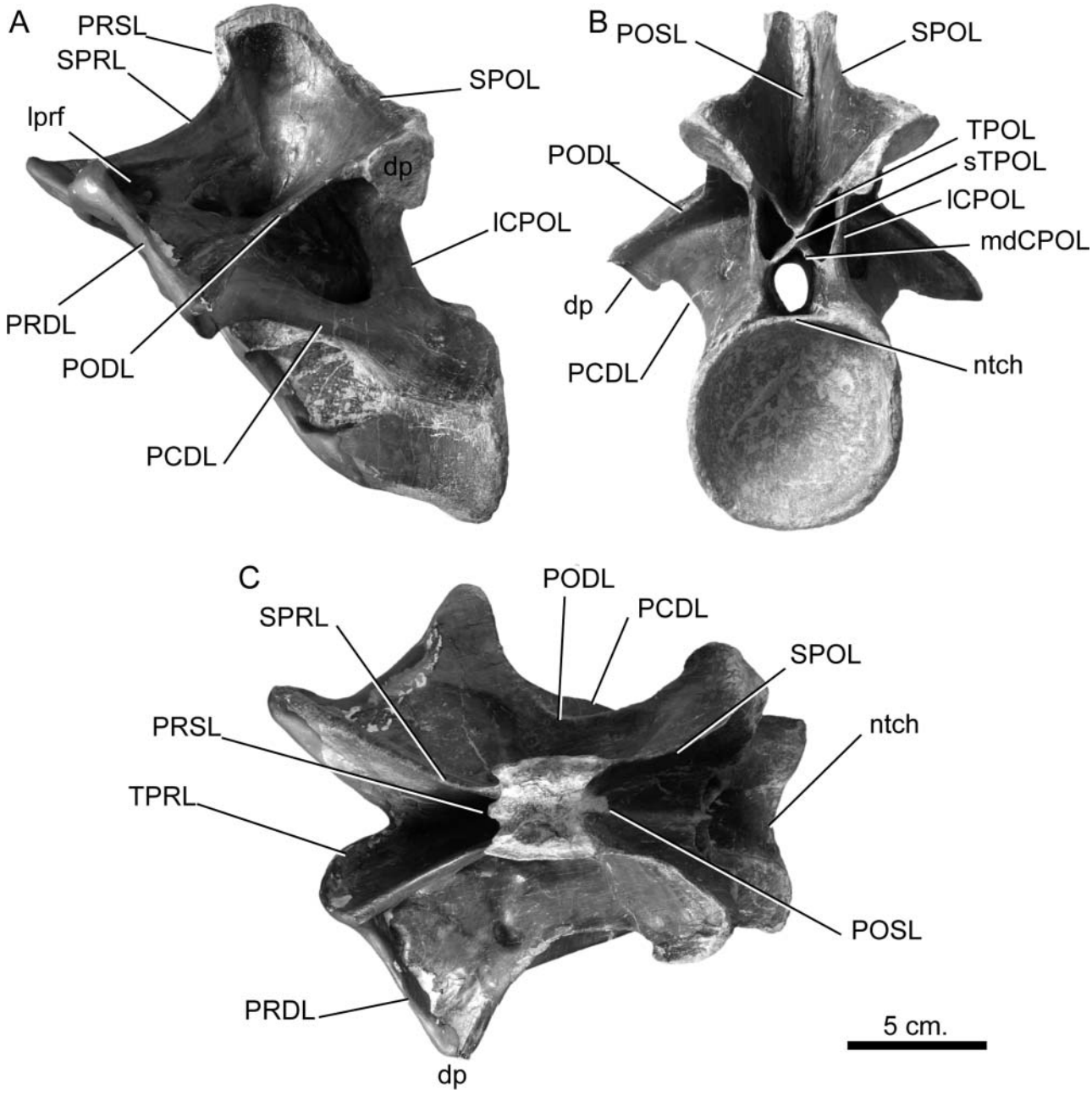

Figure 12. *Europasaurus holgeri*, mature anteroposterior cervical vertebra (DFMMh/FV 838.10) in **A,** lateral, **B,** posterior and **C,** dorsal views. See text for abbreviations.

and depth to those present in mature elements, although generally with small, vascularized areas.

Posterior cervical vertebrae. Two posterior cervicals are part of the specimen DFMMh/FV 838 and regarded as the first two posterior cervical vertebrae (DFMMh/FV 838.11c and 838.10; Figs 9A, B, E–G, 12). The presence of well-developed CPOF that are medially divided by a single and short sTPOL sets these two elements apart from the middle cervical vertebrae. The third element, represented by a broken dorsal part of a neural spine (DFMMh/FV 573.6), is regarded as one of the most posterior cervical vertebrae due to its similarity with the neural spine of the anterodorsal vertebrae (Fig. 14). The notch on the dorsal margin of the posterior articular surface, which is distinctive in the anterior and middle cervical vertebrae, is only slightly developed in the posterior cervical centra and is expressed as a shallow, but distinct, concavity (Figs 9F, 12C,

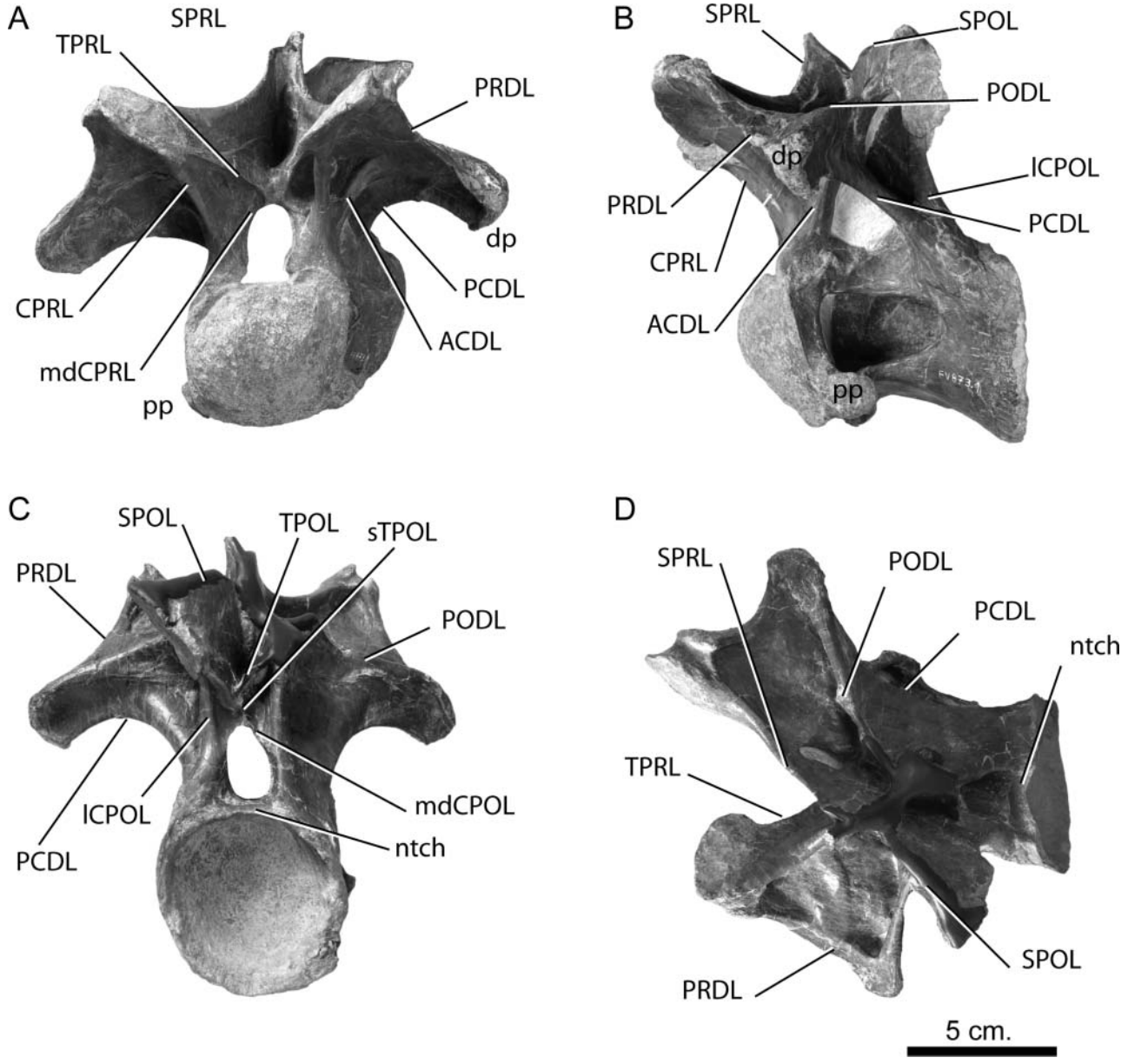

Figure 13. *Europasaurus holgeri*, mature posterior–posterior cervical vertebra (DFMMh/FV 873.1) in **A,** anterior, **B,** lateral, **C,** posterior and **D,** dorsal views. See text for abbreviations.

13D). The plane of the posterior articular surface is almost perpendicular to the long axes of the vertebra, instead of anteriorly directed as in the anterior cervical vertebrae.

The ventral side of the posterior cervical centra is slightly concave at parapophysis level, remaining almost flat over the rest of the ventral face of the centra (Fig. 9G). The capitular articulation of the parapophysis is not anterolaterally oriented as in anterior and middle cervical vertebrae, but instead faces laterally (Fig. 13B).

The pleurocoels are simple and deeply penetrate the centra, leaving a thin septum in the sagital plane, which is not wider than 3–5 mm. The pleurocoels of the most posterior cervical centra are only slightly longer than high, with internal air spaces that invade the vertebrae dorsally, forming large single camerae. The presence of camerae in cervical vertebrae is a derived character among sauropods (e.g. Wedel 2003). Among macronarians, a further derived state (presence of small internal air spaces) characterizes titanosauriforms and is probably present in the cervical vertebrae of some more basal camarasauromorphs (Carballido *et al*. 2012b). In the anteroposterior cervical vertebrae, the transverse process is strongly lateroventrally inclined (Fig. 9C, D), and the most posterior cervicals are almost completely directed laterally (Fig. 13). Ventrally, the

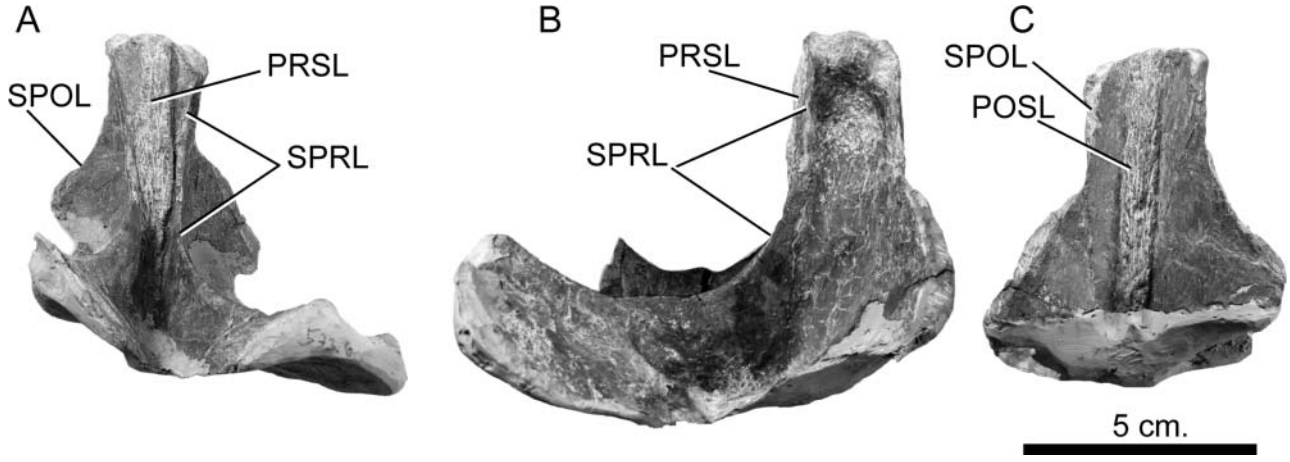

Figure 14. *Europasaurus holgeri*, mature posteriormost cervical neural spine (DFMMh/FV 573.6) in **A,** anterior, **B,** lateral and **C,** posterior views. See text for abbreviations.

transverse process is supported by the two infradiapophyseal laminae, the ACDL and the PCDL. The ACDL is still very ventrally positioned in the transverse process, but its dorsal end almost reaches the PCDL, being not as far from the diapophysis as it is in the middle cervical vertebrae. The ACDL and PCDL form the anterodorsal and posterodorsal edges of the POCDF, respectively, which is ventrally bounded by the dorsal margin of the centrum (Fig. 13B). The PRCDF is triangular in shape, with rounded points and with its base dorsally positioned (Fig. 13A).

The prezygapophyses of the most posterior cervical elements are heavily inclined, forming an angle slightly greater than 45° (Fig. 13A). In the most posterior cervicals the prezygapophyseal processes slightly surpass the anterior articular surface (Fig. 13B). The CPRL ventrally supports the prezygapophyses, but this lamina is more anterodorsally and vertically oriented than the CPRL of the anterior and middle cervical vertebrae. The CPRF is less developed than in the preceding cervical vertebrae. As a result of this paired fossae, the mdCPRL is also present, but only as a small crest bordering the neural canal and making contact dorsally with the TPRL (Fig. 13A). Thus in *Europasaurus*, the mdCPRL persists to the posterior cervical vertebrae, disappearing in the last vertebrae of the neck and being absent in dorsal vertebrae (see below). The mdCPRL persists in anterodorsal vertebrae of the titanosauriform *Chubutisaurus* (Carballido *et al.* 2011b). In the anteroposterior cervical vertebrae (DFMMh/FV 838.10 and 838.11), the height of the CPOL is about 0.65 times the height of the posterior articular surface, a ratio that is even higher in the most posterior cervical vertebrae (0.85 in DFMMh/FV 873.1; Fig. 13C). Resulting from this higher position of the postzygapophyses, the TPOL is oriented ventromedially and not flat as in the more anterior elements. In posterior cervical vertebrae, the TPOLs (left and right) converge medially, forming a vertical single TPOL (sTPOL). The sTPOL contacts the mdCPOL, just above the neural canal (Figs 9B, 12B, 13C). In posterior cervical vertebrae, the TPOL does not form the dorsal edge of the neural canal (as described for anterior and middle cervical vertebrae), but is separated from the neural canal by the sTPOL. The CPOF of the most posterior cervical vertebrae is higher but shallower than that of the anteroposterior cervical elements. Thus, as with the CPRF, the CPOF disappears in posterior cervicals, and is not present in dorsal vertebrae (see below). The mdCPOL bounds the dorsal edge of the neural canal, giving to it a triangular shape on its dorsal third part (Figs 9B, 12C). The postzygapophysis is connected laterally with the transverse process by the PODL. In the anteroposterior element, this lamina runs posterodorsally from the diapophysis down to the anteroventral aspect of the postzygapophysis. In posteriormost cervical vertebrae, the transverse process is at the same height as the postzygapophysis, and therefore the PODL is mainly directed posterolaterally (Fig. 13B). The lateral fossa below the postzygapophysis, the POCDF, is large and clearly visible in lateral view. This fossa strongly penetrates the neural arch in posterior cervical vertebrae.

Besides the neural spine of the two anteroposterior cervical vertebrae (DFMMh/FV 838.11 and 838.10c), a complete posteriormost neural spine is preserved. This neural spine (DFMMh/FV 573.6) is clearly higher than that of the anteroposterior cervical vertebra (DFMMh/FV 838.11, 838.10c), and is more similar to that of the anterodorsal vertebrae than one of the preceding cervical vertebrae. Nevertheless, the large SPRL and its inclination indicate that the neural spine corresponds to a cervical element, regarded here as one of the posteriormost cervical elements preserved (Fig. 14). The neural spine of the anteroposterior cervical vertebrae has an equal length and

width (Figs 9, 12), whereas the posteriormost neural spine is almost twice as wide as it is long. The paired neural spine laminae of the cervical vertebrae, the SPRL and the SPOL, are well developed. The PRSL is present as a narrow ridge in the anteroposterior vertebrae, whereas in the posteriormost neural spine it is visible as a wider, rough lamina, which is bounded closely by the SPRLs. Therefore, cervical vertebrae of *Europasaurus* are characterized by the presence of a PRSL, an autapomorphy of *Europasaurus* convergently acquired in *Isisaurus* (Wilson & Upchurch 2003). In posterior cervical vertebrae, the SPOL is mainly directed dorsally, and the SPOF is a shallow fossa. The dorsal edge of the neural spine does not show any lateral expansion, being only half of the distance between the lateral edges of the postzygapophyses. A distinctive expansion in the neural spine of posterior cervical vertebrae was described for some titanosauriforms (e.g. *Mendozasaurus*; González Riga 2005).

Dorsal vertebrae

The dorsal elements known in *Europasaurus* include some complete dorsal vertebrae, juvenile centra and neural arches, and some isolated and more fragmentary elements. As with other sauropod necks, complete dorsal series are uncommon, and although *Europasaurus* can be regarded as having 12 dorsal vertebrae (the plesiomorphic condition in Macronaria; Wilson & Sereno 1998; Upchurch *et al.* 2004), the number of dorsal vertebrae is unknown for this genus. Throughout the dorsal series, several changes can be observed from the anterior to the posterior vertebrae. These changes are used to classify the dorsal vertebrae into three main categories. The anterodorsal vertebrae are identified by the low parapophysis (still connected to the centrum), the absence of mCPOL, and lack of the hyposphene–hypantrum extra joint. The last anterodorsal vertebra is similar except for having a hyposphene and not a hypantrum. Middle dorsal elements are recognized by the intermediate position of the parapophysis, the presence of both hyposphene and hypantrum articulations, and by the weakly developed mCPOL. Posterior dorsal vertebrae have a high parapophysis, which is positioned dorsally and divides the PRDL into two laminae, the PRPL and the PPDL. The general shape of the centra and pleurocoels and the orientation of the laminae were used to identify the incomplete elements, comparing them with more complete dorsal vertebrae.

Anterodorsal vertebrae. Five anterodorsal elements are preserved, including: a complete centrum with the parapophysis at the pleurocoel level (DFMMh/FV 894); a complete vertebra without a hypantrum, but with a well-developed hyposphene sustained from below by a single TPOL (DFMMh/FV 1048); the posterior half of a vertebra with a well-developed hyposphene sustained from below by a single TPOL (DFMMh/FV 833.4); and the distal part of a neural spine (DFMMh/FV 550.1).

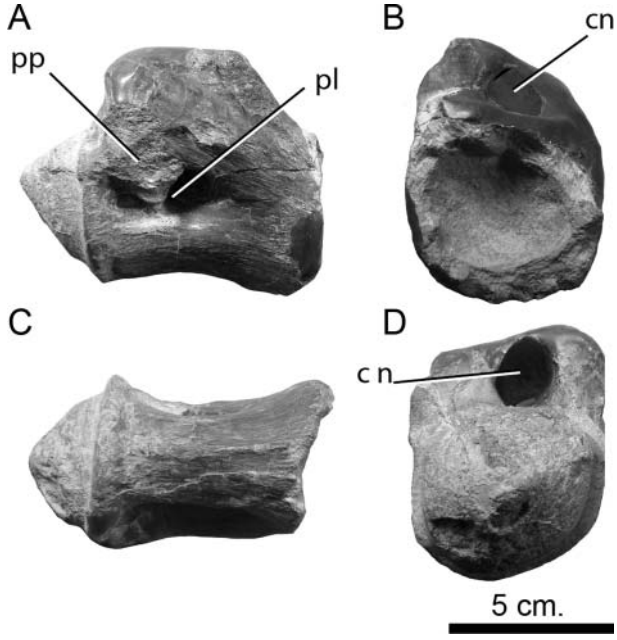

Figure 15. *Europasaurus holgeri*, mature anterodorsal centrum (DFMMh/FV 894) in **A,** lateral, **B,** posterior, **C,** ventral and **D,** anterior views. See text for abbreviations.

The centrum DFMMh/FV 894, which is broken just above the pedicel level (Fig. 15), is interpreted as the anteriormost preserved dorsal element. It is strongly opisthocoelous (Fig. 15). The anterior articular ball does not occupy the complete centrum but is surrounded by a step (Fig. 15D). Lengthwise, the centrum is ventrally convex and not flat as in cervical vertebrae (Fig. 15C). The dorsoventrally large parapophysis is still connected to the centrum, and situated at pleurocoel level (Fig. 15A). A similar parapophysis position is observed in the first two dorsal vertebrae of other sauropods (e.g. *Camarasaurus*, *Euhelopus*; Osborn & Mook 1921; Wilson & Upchurch 2009). We interpret this centrum as one of the anteriormost vertebral elements of *Europasaurus*, probably the first or second dorsal vertebra.

When comparing the most complete anterodorsal vertebra (DFMMh/FV 1048) with other basal macronarians (e.g. *Camarasaurus*, *Brachiosaurus*; Osborn & Mook 1921; Riggs 1904), the low position of the parapophysis, the absence of the hypantrum and the well-developed hyposphene indicate that this element is an anterodorsal vertebra, probably the third or fourth dorsal element of *Europasaurus*. This vertebra is the most complete anterodorsal element, and thus the description is mainly based on it.

The opisthocoelous centrum of DFMMh/FV 1048 is almost as long as posteriorly wide (Online Supplementary Material; Fig. 16), with rounded articular surfaces. The ventral aspect of the centrum is similar to the anterior centrum described above (Fig. 16C). The parapophysis is large and drop-shaped, almost four times higher

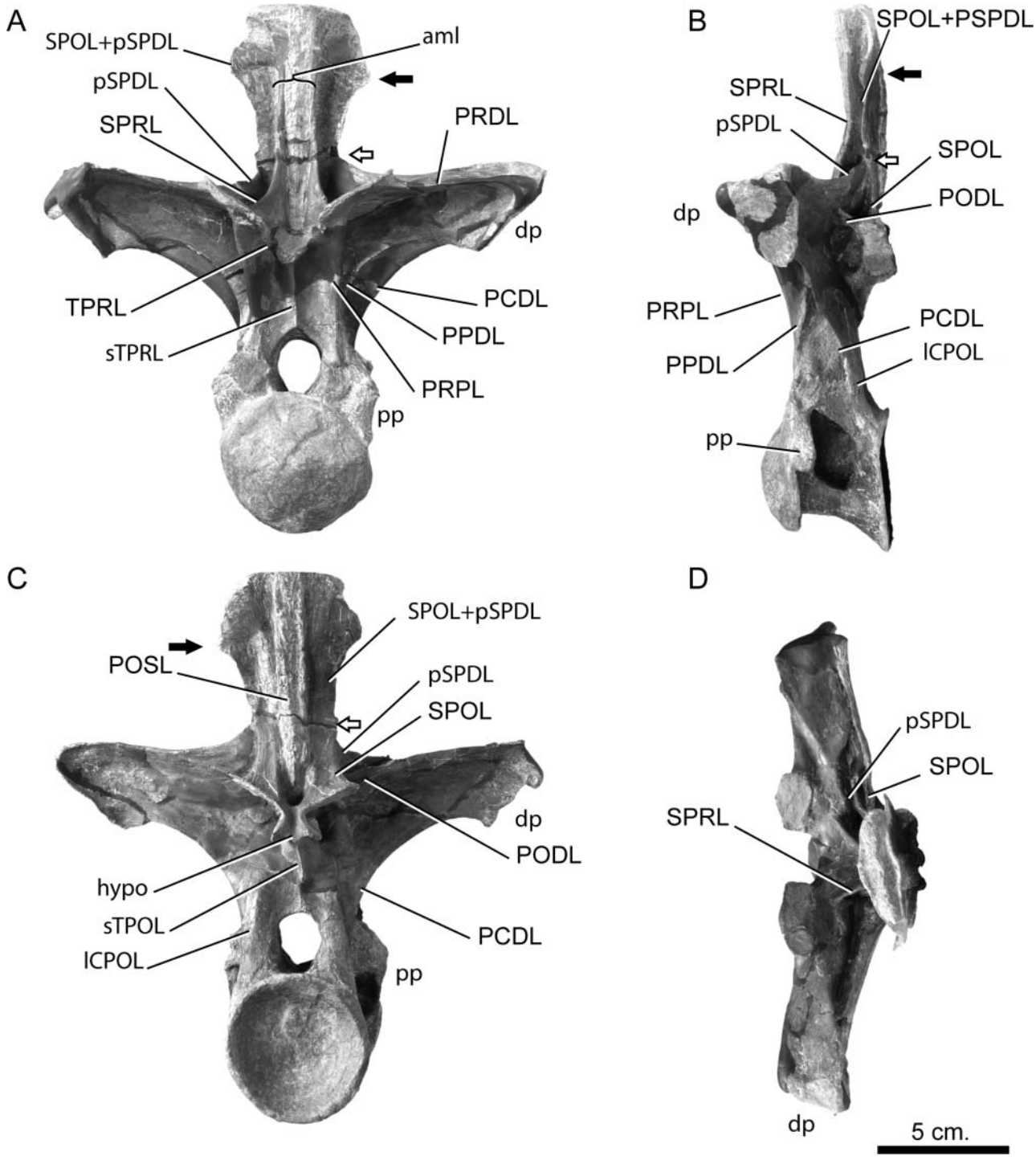

Figure 16. *Europasaurus holgeri*, mature anterodorsal vertebra (DFMMh/FV 1048) in **A,** anterior, **B,** lateral, **C,** posterior and **D,** dorsal views. The black arrow shows the position of the triangular aliform process and the unfilled white arrow with black border shows the point of junction of SPOL and pSPDL. See text for abbreviations.

than wide, and placed between the centrum and the neural arch. This position interferes with the laminae that link the prezygapophysis and diapophysis with the anterior aspect of the centrum and the anterior margin of the pleurocoel (Fig. 16B). The single and large pleurocoel opens internally into large internal paired camerae, which seem to reach the neural arch. Therefore, the internal structure of the anterodorsal vertebrae of *Europasaurus* is similar

to the camerate air spaces of basal camarasauromorphs, such as *Camarasaurus* (Wedel 2003), *Galvesaurus* (Barco *et al.* 2006) and *Giraffatitan* (Janensch 1947). Nevertheless, and contrary to these sauropods, the internal camera in *Europasaurus* does not reach the middle and posterior dorsal centra but is restricted to anterior and anterior middle dorsal vertebrae.

When aligning the neural canal with the horizontal axis in lateral view, the diapophysis of this vertebra is at the same vertical level as the parapophysis (Fig. 16B), a widespread character among sauropods (Upchurch *et al.* 2004). The diapophysis is large and triangular-shaped, with its base positioned dorsally and facing ventrolaterally. Two well-developed laminae connect the diapophysis with the centrum, the PCDL and the PPDL, which form the ventral support of the transverse process. As the parapophysis is restricted almost entirely to the neural arch, the lamina that runs anteroventrally from the diapophysis to the centrum is the paradiapophyseal lamina (PPDL) and not the ACDL. Thus, as in other sauropods (Wilson 1999), the ACDL is only present in cervicals and anteriormost dorsal vertebrae of *Europasaurus*, in which the parapophysis is still in the centrum, as was described for the isolated anteriormost centrum. The PPDL runs posterodorsally from the dorsal margin of the parapophysis and connects the PCDL below the diapophysis. Because of this arrangement, the lateral fossae below the zygapophysis line are bounded by different laminae. The CDF, enclosed by the two infradiapophyseal laminae (PCDL and PPDL), is triangular-shaped and a small pneumatopore-like opening is positioned dorsally. This opening has a rounded and well-defined ventral margin, and opens anteroventrally into the neural arch. The PRCDF has the shape of an inverted triangle with its base oriented dorsally (Fig. 16A, B). In this vertebra, and even more in the following dorsal vertebrae, the PRCDF is positioned anterodorsally in the neural arch, below the prezygapophysis. Although the PRCDF excavates deeply into the neural arch, no communication with any internal pneumatic cavity is present, and thus this fossa finishes without any internal expansion. Therefore, in *Europasaurus*, only the CDF seems to show a communication with the neural arch. The diapophysis is linked with the prezygapophysis by an almost horizontal and lateral directed PRDL. The PRDL runs from the dorsolateral aspect of the prezygapophysis up to the anterodorsal point of the diapophysis. Two laminae are directed posteriorly from the diapophysis, the SPDL (posterodorsally) and the PODL (posteriorly). The PODL persists as a very weakly developed lamina, visible in lateral and posterior views (Fig. 16B, C), which runs from the anterolateral margin of the postzygapophysis (as is in cervical vertebrae) to the dorsal margin of the transverse process. In dorsal vertebrae, this lamina does not reach the diapophysis but contacts the SPDL in the posterior edge of the transverse process. Therefore, the posterior edge of the transverse process is formed by a composite lamina (PODL + SPDL; Fig. 16B, C).

In anterior view, the prezygapophyses are inclined ventromedially, forming an angle similar to that observed in posterior cervical vertebrae (40°). The prezygapophyses are flat and oval-shaped, with the longer margin positioned lateromedially. At their medial edge, the prezygapophyses do not show any kind of lateroventral expansion, and thus the hypantrum is absent in this vertebra. Both prezygapophyses are linked by robust paired TPRLs, which are directed ventromedially from the prezygapophysis to the midline of the vertebra. The middle contact of the TPRLs produces a single and ventrally directed lamina, the single TPRL (sTPRL). The sTPRL links the paired TPRLs median contact with the dorsal edge of the neural canal (Fig. 16A), which is oval-shaped. The prezygapophysis is connected ventrally with the parapophysis and not with the centrum because the dorsal half of the parapophysis is no longer situated on the centrum (Fig. 16A, B). Therefore, the CPRL of cervical vertebrae is replaced by its dorsal counterpart, the prezygoparapophyseal lamina (PRPL; Wilson 1999). The PRPL is large, thin and oriented vertically in this vertebra. The PRPL (which replaces the CPRL in anterodorsal vertebrae) remains as an undivided lamina. The CPRF is present in anterior view, below the prezygapophyses. This fossa is bounded laterally by both CPRL (left and right), which run parallel to each other. The single median strut below the prezygapophyses (the sTPRL) slightly divides the CRPF into left and right areas (Fig. 16A).

The postzygapophyses are oval-shaped and lateromedially long. In posterior view, the most notable characteristics of this vertebra are the weak development of the paired lCPOL (well developed in cervical vertebrae) and the presence of a robust hyposphene (Fig. 16C). The hyposphene is supported ventrally by a single and thin lamina (the sTPOL). The sTPOL runs from the ventral margin of the hyposphene, diminishing ventrally but reaching the dorsal edge of the neural canal. The sTPOL, which first appears in posterior cervical vertebrae, persists up to the anterodorsal vertebrae, and is present below the first vertebra with the hyposphene in *Europasaurus*. This lamina is not present in more posterior dorsal vertebrae, differing from the condition of diplodocids (e.g. Upchurch *et al.* 2004) or *Tehuelchesaurus* (Carballido *et al.* 2012b). The paired lCPOL is recognized as a convex, low ridge, which runs from the centrum up to the height of the hyposphene. The position and orientation of this lamina indicate that it is the relict lCPOL, which forms the ventral pillars below the postzygapophyses of cervical vertebrae. Below the hyposphene, no paired laminae are observed, thus the mCPOL, present in more posterior dorsal vertebrae (see below), is absent in anterodorsal elements. In lateral view, the POCDF is present as a small but deep fossa. This fossa almost reaches the most medial part of the neural arch and is bounded

posterolaterally by the relict lCPOL and the hyposphene (Fig. 16B, C).

The neural spine of this element is markedly wider than anteroposteriorly long, and is petal-shaped in anterior and posterior views, with a developed triangular lateral process or 'aliform process' (Upchurch 1995; Fig. 16A, C). The triangular lateral process is wider than the posterior articular surface and equally wide as the anterior articular surface's maximum width. The SPRLs are directed dorsomedially from the posteromedial edge of the prezygapophyses up to the first quarter height of the neural spine. From this height these laminae run parallel to each other up to the dorsal end of the neural spine where they widen laterally (Fig. 16A). The SPRLs laterally bound a medial wide rough lamina, forming a composed anterior median lamina (aml; Fig. 16A). A similar rough lamina is present in some other sauropods (e.g. *Haplocanthosaurus*, CM 572; *Bellusaurus*, IVPP V8299). The position and texture of this median lamina allows us to recognize it as the PRSL, also present in the cervical vertebrae of *Europasaurus* (see above). The shape, rough surface texture and development of the PRSL resemble that of its posterior counterpart, the POSL, and thus both single laminae are equally developed in the presacral vertebrae of *Europasaurus*. The PRSL runs from the ventral margin of the neural spine up to its dorsal end, differing from the short and triangular morphology of the PRSL present in some basal titanosauriforms (e.g. *Brachiosaurus*, FMNH 25107) and from the narrow and smooth PRSL widely distributed among the more derived clade of titanosaur (Salgado *et al.* 1997). Therefore, the median lamina present in the anterior surface of the dorsal vertebra is a composite lamina formed by the SPRL and a long and rough PRSL (Fig. 16A).

Thus, the anterior median lamina of *Europasaurus* resembles that of other basal macronarians (e.g. *Bellusaurus*, IVPP V8300; *Euhelopus*, PMU 233; *Galvesaurus*, CLH-16) and differs from the anterior median lamina, with a short and triangular-shaped PRSL in some non-neosauropods (e.g. *Mamenchisaurus*; He *et al.* 1996), the basal macronarian *Haplocanthosaurus* (CM 879), and brachiosaurids (*Giraffatitan*, HMN-MB SII; *Brachiosaurus*, FMNH 25107).

As was noted above, two laminae, the weakly developed PODL and the SPDL, run posteriorly from the diapophysis. Due to its position, the SPDL lamina is recognized as the pSPDL, following Salgado & Powell (2010). The pSPDL differs from the anterior SPDL (aSPDL) because of its different origin and position in the spine and transverse process. A very small juvenile neural arch, identified as a middle dorsal element, also supports the interpretation of a posterior ontogenetic origin of the SPDL in *Europasaurus* (see below). The pSPDL contacts the SPOL very low in the neural spine in this vertebra and in the following dorsal elements. As a result of this contact, a composite lamina, formed by the union of the pSPDL and the SPOL, is exposed laterally in the neural spine. The pSPDL–SPOL union is placed at the ventral third height of the neural spine, thus slightly ventral to the lateral expansion of the neural spine (Fig. 16B, C). The ventral position of this contact differs from the more dorsal contact, and this is a feature widely distributed among sauropods (e.g. *Bellusaurus*, IVPP V8299; *Euhelopus*, PMU 233, especially in titanosaurs; Salgado & Powell 2010) and resembles more the condition present in *Giraffatitan* (FMNH P 25107). In posterior view, the neural spine is formed by the single POSL, which, like the PRSL, is a wide and rough lamina. The SPOF, which is a large and well-developed fossa in cervical vertebrae, is also present in anterodorsal vertebrae. Nevertheless, the fossa is extremely reduced in this anterodorsal vertebra, persisting as a very small middle fossa above the hyposphene and between both postzygapophyses (Fig. 16C). The POSL runs from the deep part of this fossa up to the dorsal end of the neural spine.

Mature middle dorsal vertebrae. The preserved mature middle dorsal vertebrae elements (Figs 17, 18) include an anterior third of a transversely broken vertebra (DFMMh/FV 835), an almost complete vertebra, which is missing the left transverse process and the neural spine (DFMMh/FV 1049), and a partially broken vertebra (DFMMh/FV 787). None of the middle dorsal vertebrae elements are complete; all are missing most of the neural spine, which is well preserved in immature elements (see below). The following description is mainly based on the more complete element (DFMMh/FV 1049; Fig. 17).

The relatively short centum indicates an anterior position in the middle dorsal vertebrae, as the shorter dorsal centrum of other sauropods is commonly present around the fifth dorsal (e.g. *Camarasaurus*, *Trigonosaurus*; Osborn & Mook 1921; Campos *et al.* 2005). Therefore, this vertebra is identified as one of the first middle dorsal vertebrae, probably the fifth dorsal of *Europasaurus*. The centrum is opisthocoelous, and the convex anterior surface is not as well developed as in anterodorsal vertebrae. The ventral aspect of the centrum is not as convex as in anterodorsal vertebrae, although it is slightly convex. The pleurocoel of this vertebra is extremely high, being around twice as high as it is wide, with its highest point positioned anteriorly (Fig. 17B). As in anterodorsal vertebrae internal camerae are present, with the anterodorsal excavation surpassing the neurocentral suture and indeed penetrating the neural arch. The parapophysis is almost twice as high as it is wide and is clearly completely disconnected from the centrum (Fig. 17A, B). The replacement of the ACDL and CPRL by the PPDL and PRPL (Wilson 1999) occurs in two stages, as is also observed in most sauropods (e.g. *Camarasaurus*, *Amargasaurus*; Osborn & Mook 1921; Salgado & Bonaparte 1991; MACN–N 15). First, the ACDL and the CPRL are respectively replaced by the PPDL and PRPL, as these laminae are connected with the parapophysis and not

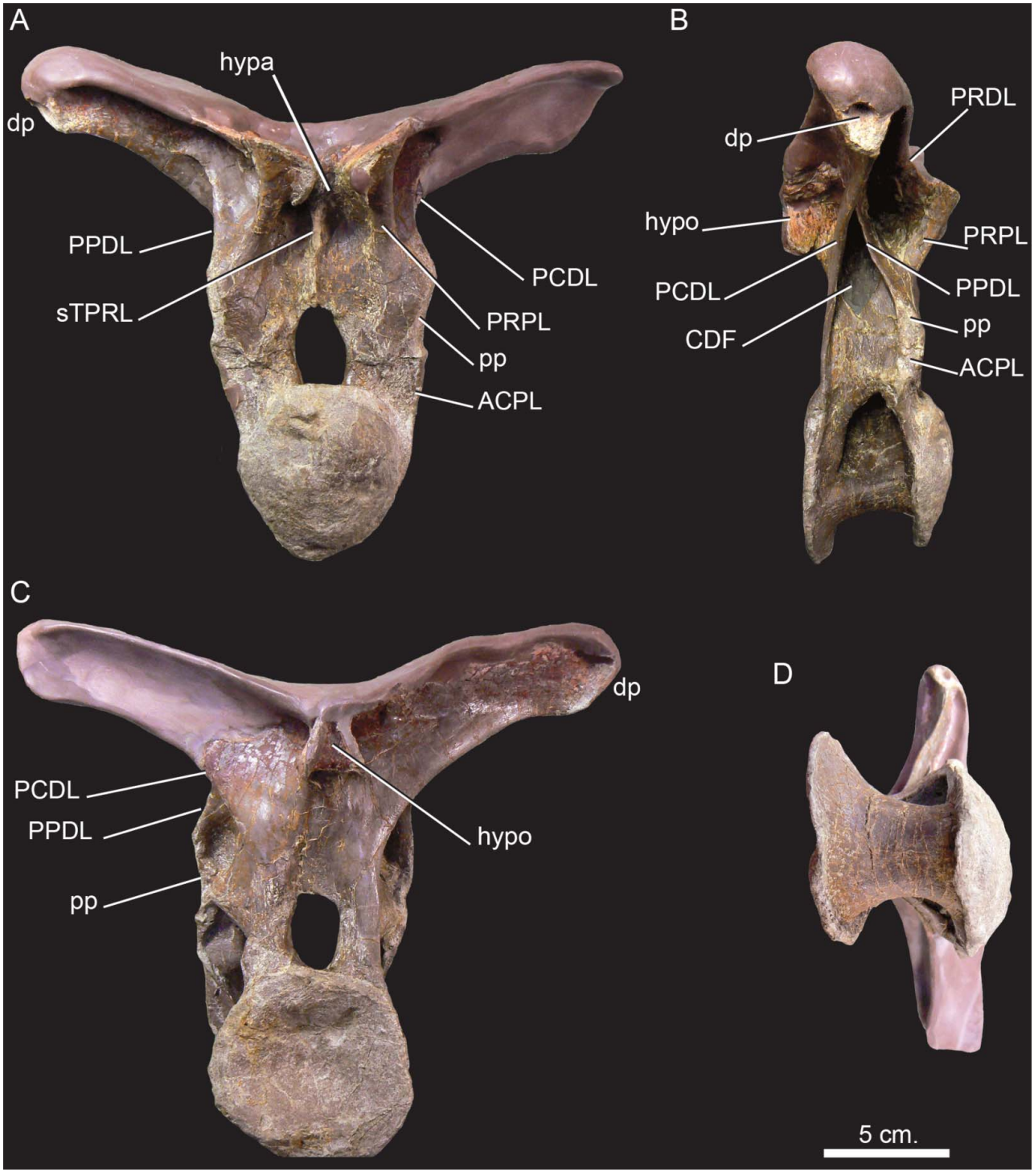

Figure 17. *Europasaurus holgeri*, mature middle dorsal vertebra (DFMMh/FV 1049) in **A,** anterior, **B,** lateral, **C,** posterior and **D,** ventral views. See text for abbreviations.

with the centrum. This first stage is present in anterodorsal vertebrae, whereas in middle dorsal vertebrae, the parapophysis is completely out of the centrum and communicates with the centrum by the anterior centroparapophyseal lamina (ACPL), which is not present in anterodorsal vertebrae. The ACPL is a single and vertical lamina, which forms the anterodorsal edge of the high pleurocoel (Fig. 17B). The PRPL is anterodorsally directed from the parapophysis up to the lateroventral margin of the zygapophysis. The CDF and PRDF are present and well developed in this vertebra.

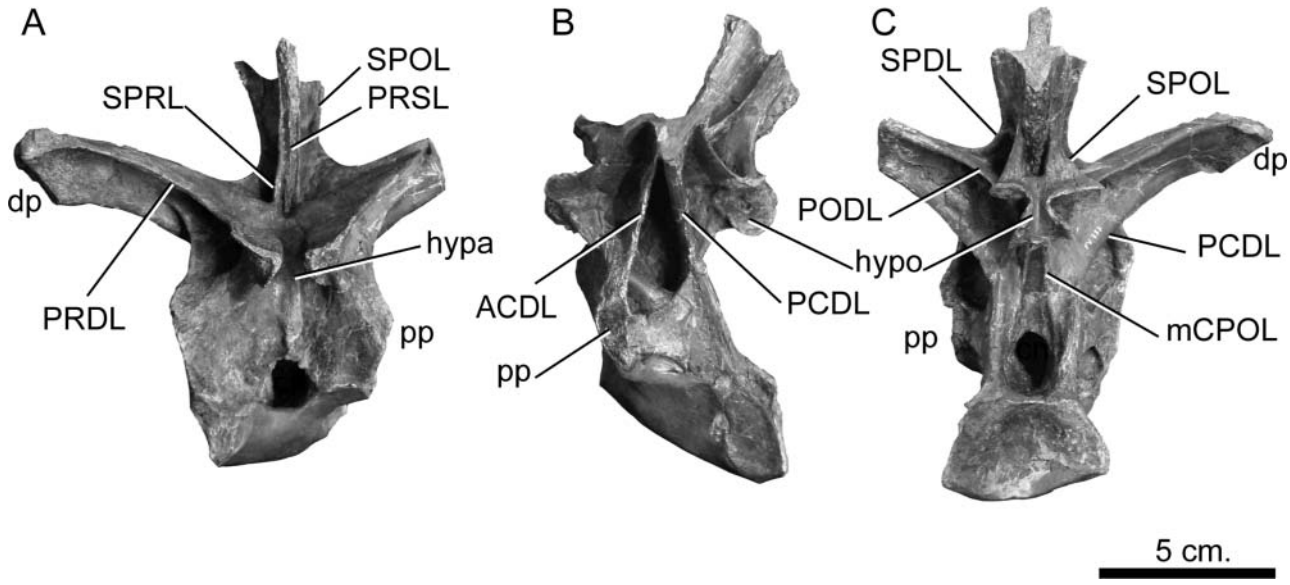

Figure 18. *Europasaurus holgeri*, mature posterior–middle dorsal vertebra (DFMMh/FV 787) in **A,** anterior, **B,** lateral and **C,** posterior views. See text for abbreviations.

Instead of having a similar size, as in anterodorsal vertebrae, the PRDF is relatively smaller and less developed than the CDF. The CDF is bounded by the PCDL posteriorly, the PPDL anteriorly, and the parapophysis anteroventrally (Fig. 17B). A deep and well-delimited excavation is observed inside the CDF. This deep excavation of the CDF expands internally into the neural arch, thus the term centrodiapophyseal fossa pneumatopore (CDF pneumatopore) is used here to refer to it. Therefore, a supraneural camera extends into the ventral part of neural arch. Similar supra-

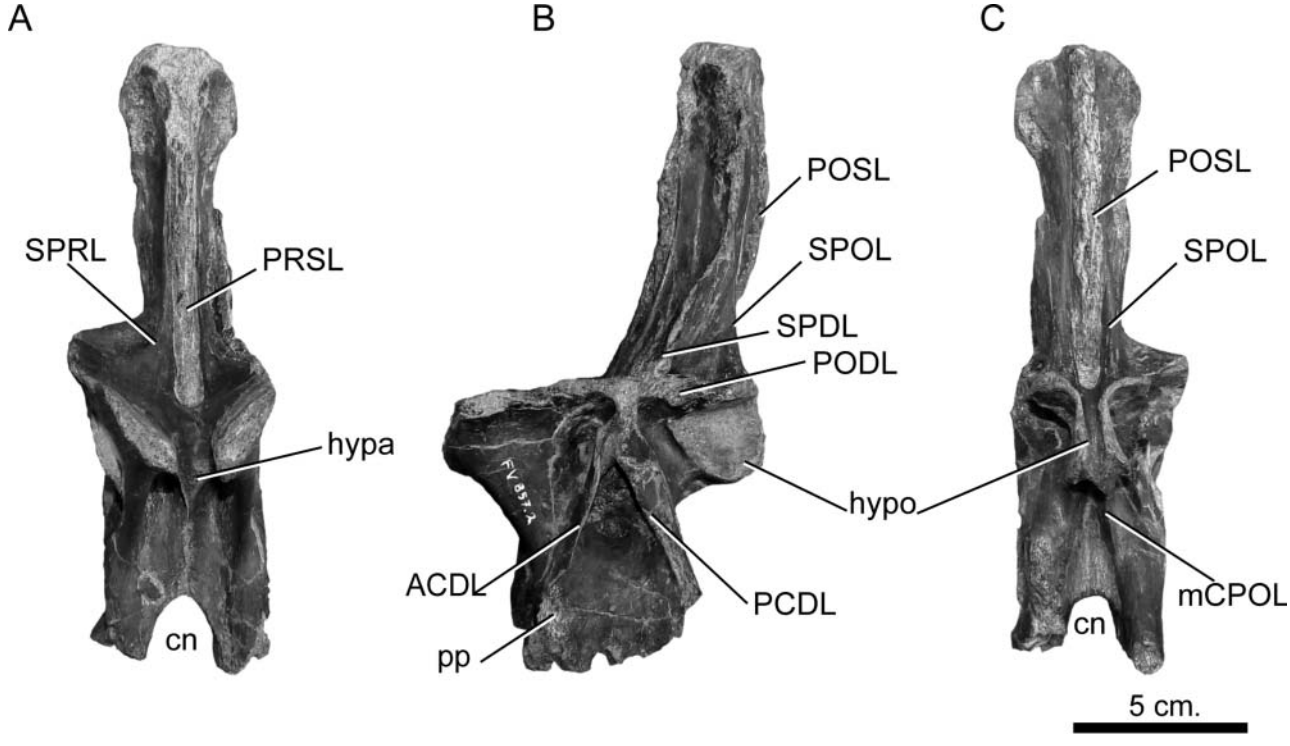

Figure 19. *Europasaurus holgeri*, immature middle dorsal vertebra (DFMMh/FV 857.2) in **A,** anterior, **B,** lateral and **C,** posterior views. See text for abbreviations.

neural camerae have been described for the basal sauropods *Barapasaurus* and *Cetiosaurus* (Bonaparte 1999; Upchurch & Martin 2003) and the basal macronarian *Tehuelchesaurus* (Carballido *et al.* 2012b) and *Camarasaurus* (Bonaparte 1999). The ventral margin of this pneumatopore is well marked, with a rhomboidal shape in lateral view (Figs 17B, 18B). The deep invasion of this pneumatopore into the centrum results in a thin median lamina, which separates both (left and right) CDF pneumatopores. The PRCDF is delimited dorsally by the PRDL, anteroventrally by the PRPL and posteroventrally by the PPDL, as was described for the complete anterodorsal vertebra. In lateral view, the PRCDF is located below the prezygapophysis and the transverse process, and does not open into internal camerae. As in other non-titanosauriform sauropods (cf. *Tehuelchesaurus*; Carballido *et al.* 2012b), the PCDL is not ventrally expanded.

Whereas anterodorsal elements miss the hypantrum, in this vertebra the prezygapophysis are expanded laterally, forming an anterior accessory joint, which articulates with the hyposphene of the preceding dorsal vertebra. A product of the hypantrum, the TPRL is not present in this vertebra, a common change in all sauropods (Wilson 1999). Nevertheless, a single and medially positioned crest is observed above the neural canal (Fig. 17B), which is interpreted as the relict sTPRL, better developed in anterodorsal elements.

The lateral articulation surfaces of the hyposphene are separated by a medial depression. The sTPOL, which commonly disappears with the first hyposphene, is missing in middle and posterior dorsal vertebrae of *Europasaurus*. Among neosauropods, the sTPOL was convergently acquired by diplodocids (Upchurch *et al.* 2004) and *Tehuelchesaurus* (Carballido *et al.* 2012b). The lCPOL, observed in anterodorsal vertebrae and the mCPOL and well developed in posterior dorsal vertebrae, are not developed in this element. Instead, an incipient mCPOL is present, which bounds the neural canal and approaches the hyposphene as a smooth convexity (Fig. 17). Although no neural spine is preserved in DFMMh/FV 1049, a segment of the neural spine can be seen in DFMMh/FV 787, which is interpreted as having a slightly more posterior position. This position is supported by its relatively low parapophysis but well developed mCPOL (Fig. 18). The neural spine does not differ greatly from that of anterodorsal vertebrae. The pSPDL splits from the PODL on the posterior side of the transverse process and contacts the SPOL relatively ventrally, and the PRSL and POSL are well developed but in this vertebra are slightly narrower.

Immature middle dorsal elements. Three immature middle dorsal neural arches (Figs 19, 20) were recovered (DFMMh/FV 857.2, 243 and [1032, 1072]). They show some morphological differences that deserve to be described and compared with the previously described middle dorsal vertebra. These three elements can be identified as showing three different ontogenetic stages.

The first of these elements (DFMMh/FV 857.2; Figs 19A–C) is the largest of the three neural arches. It is damaged on the lateral side, missing most of its transverse process and the parapophysis (Fig. 19B). This neural arch is regarded as a posterior middle dorsal vertebra, due to the low parapophysis, the orientation of the PPDL and the presence of weakly developed mCPOL (Fig. 19A–C). The element does not differ significantly from the mature middle dorsal vertebrae described above. All the major fossae and laminae present in mature elements can be recognized and are well developed. The CDF is deeply excavated below the diapophysis, but this excavation does not penetrate the neural arch, and thus the supraneural camerae are not present on it. The neural spine is formed by all the laminae observed in mature elements. The PODL and the pSPDL are equally developed. The pSPDL contacts the SPOL dorsally, forming the lateral composed lamina (pSPDL + SPOL), which forms a weakly developed lateral expansion or triangular aliform process. The triangular aliform process is not as laterally expanded as in mature elements, although the neural spine has an equal length and width relation (Fig. 19).

The other two preserved neural arches are significantly smaller than the one described above, with DFMMh/FV 243 being slightly larger than specimen 1032–1072. The former element is interpreted as representing a later ontogenetic stage. The parapophysis of DFMMh/FV 243 is situated entirely at the pedicel level on the ventral edge of the neural arch, indicating that this element does not belong to an anterodorsal vertebra, as evidenced by the presence of both hyposphene–hypantrum and extra joints. The ventral position of the parapophysis can be interpreted as resulting from an anterior position among middle dorsal vertebrae. Nevertheless, the absence of sTRPL (present in anterodorsal vertebrae) and the presence of well-developed paired mCPOLs (present in posterior middle and posterior dorsal vertebrae) indicate a more posterior position for this element. Therefore, DFMMh/FV 243 is regarded as a posterior middle dorsal vertebra and its low position of the parapophysis is interpreted as due to the early ontogenetic stage of this element. A higher position of the parapophysis can be expected as a late ontogenetic stage, resulting from the growth of the neural arch from the pedicels. In lateral view, the CDF and PRCDF can be observed. The CDF of this element is bounded by the PPDL and the PCDL. In contrast to the anterior and middle dorsal elements previously described, this fossa does not have any distinctive deep excavation, which was identified in mature elements as the CDF pneumatopore. The absence of this pneumatopore is interpreted as resulting from the ontogenetic stage of this element. The diapophysis is connected to the postzygapophysis by a well-developed PODL. The PODL bounds the posterior aspect of the transverse process

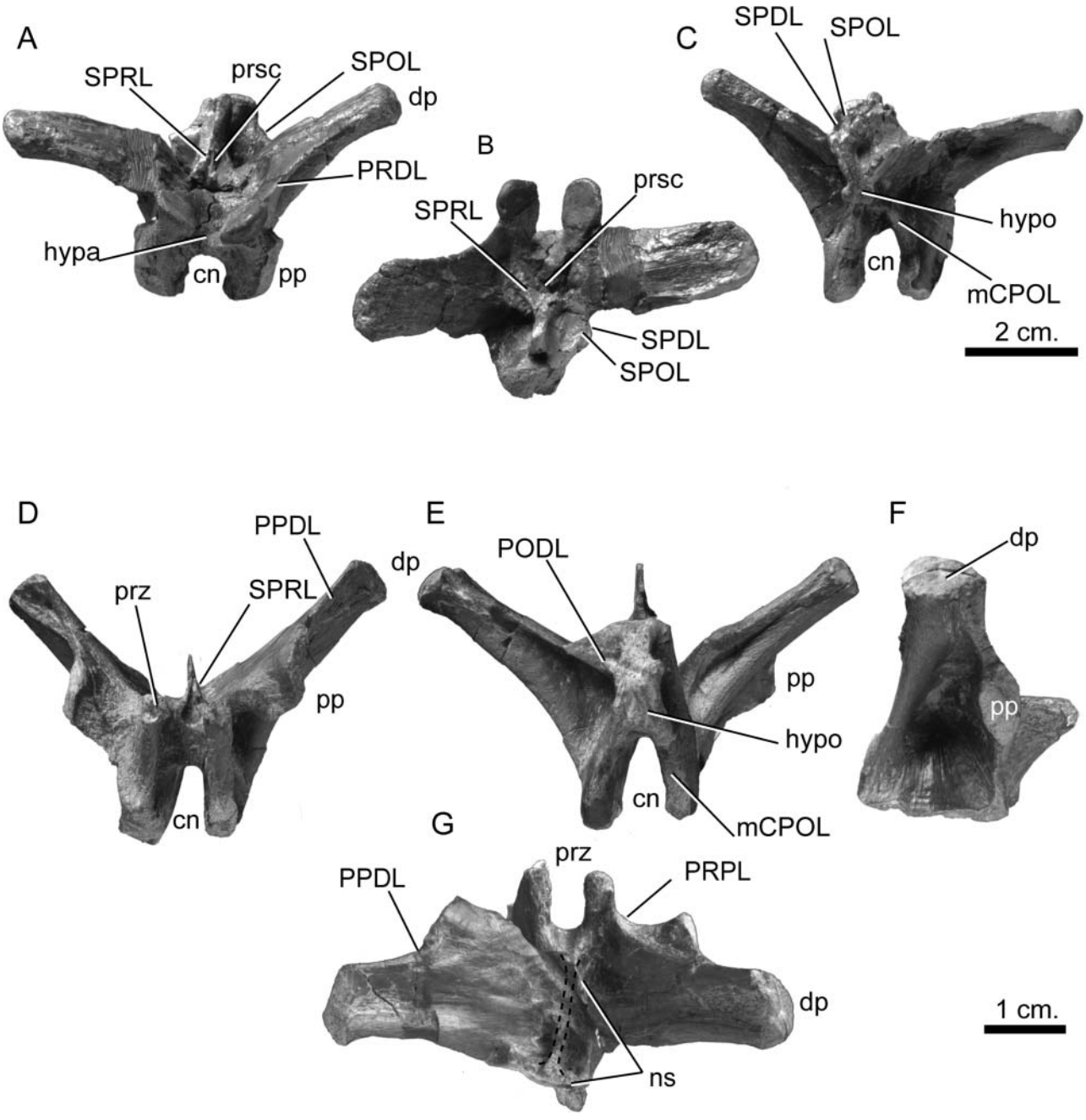

Figure 20. *Europasaurus holgeri*, immature middle dorsal vertebra. **A–C,** DFMMh/FV 243 in **A,** anterior, **B,** dorsal and **C,** posterior views. **D–G,** DFMMh/FV (1072+1048) in **D,** anterior, **E,** posterior, **F,** lateroventral and **G,** dorsal views. See text for abbreviations.

and contacts the dorsal margin of the postzygapophysis. A very narrow lamina arises from the PODL, close to the transverse process, and runs up to the neural spine. This narrow lamina (the pSPDL) is incorporated into the neural spine, and contacts the SPOL in a very ventral position. The pSPDL is weakly developed and only recognizable by the presence of a shallow fossa between it and the SPOL. Whereas in this element the pSPDL is less developed than the PODL, in all the preserved mature elements, the pSPDL is always more developed than the PODL. Therefore, in this juvenile neural arch, the SPDL seems to originate as a division of the PODL, and is thus interpreted here as a pSPDL, as was defined by Salgado & Powell (2010). As in other dorsal vertebrae of *Europasaurus*, the pSPDL contacts the SPOL to form a composite lateral lamina (pSPDL + SPOL), which forms the lateral edge of the

neural spine. In this juvenile neural arch, the neural spine is not as wide as that of mature elements, but is slightly longer than wide. In anterior view, the neural spine is formed by the paired SPRL and a low and rough prespinal scar, which is not considered to be a lamina due to its extremely low development. The paired SPRL and the prespinal scar converge medially at half the height of the neural spine. The prespinal scar, easily recognized ventrally, cannot be distinguished from the SPRL in the dorsal end of the neural spine. The neural spine is damaged posteriorly and thus the presence of a POSL cannot be determined due to preservation, but a similar development to that observed in the PRSL is expected. The SPOF is present but extremely reduced in this neural arch.

The second small immature neural arch (DFMMh/FV (1048–1072)) is identified as a posterior middle or an anteroposterior dorsal vertebra due to the high position of its parapophysis and the presence of weakly developed PRDL. The neural arch is broken into two halves and two different numbers were used for each fragment, DFMMh/FV 1058 for the left and DFMMh/FV 1072 for the right half. In anterior view, both prezygapophyses are completely preserved (Fig. 20D). The paired CPRL is well developed and bounds the CPRF. A weakly developed PRDL runs from the prezygapophysis and posteriorly contacts the diapophysis.

The postzygapophyses are damaged but a stout expansion can be observed, which is recognized as part of the hyposphene. The hyposphene is supported ventrally by well-developed, paired mCPOL (Fig. 20E). As in the previously described element DFMMh/FV 243, the dorsal face of the transverse process is completely smooth, lacking the excavations present in mature elements (Fig. 20F).

The neural spine of DFMMh/FV (1048–1072) is incompletely preserved, but most of its laminae are discernible. The SPRL is a very low lamina, in which a shallow depression occurs in the ventral part. The PRSL, which was described for mature and immature elements, cannot be recognized in this neural arch, and is thus regarded as absent. Instead, the left and right SPRL are fused together to form a single lamina (Fig. 20D). Therefore, neither the PRSL nor the prespinal scar is present in this element. At this level the neural spine is extremely thin, with a lateromedial width of only 0.09 mm. The SPDL cannot be properly recognized, and is considered absent in this element. The SPOL and the POSL cannot be observed due to preservation, but in posterior view, the dorsal half of the neural spine is preserved as a single lamina. Although it cannot be observed (due to preservation), the POSL lamina was probably absent as is the PRSL. In this neural arch of *Europasaurus*, the neural spine length is 0.64 mm, approximately seven times longer than wide. Therefore, the morphology of the neural spine in this early juvenile specimen is extremely simple, resembling the condition of basal sauropodomorphs and juveniles of more derived sauropods such as the early juvenile sauropod SMA 0009 from the Morrison Formation (Carballido *et al*. 2012a) in which the neural spine is anteroposteriorly longer than ventromedially wide.

Posterior dorsal vertebrae. Several posterior dorsal vertebra elements were collected, including: two complete dorsal vertebrae (DFMMh/FV 712.1 and DFMMh/FV 652.4), a fragmentary neural arch (DFMMh/FV 890.1), a complete neural spine (DFMMh/FV 007), two almost complete centra with the ventralmost part of the neural arch (DFMMh/FV 580.2 and DFMMh/FV 012), one complete centrum (DFMMh/FV 019), and a fragmentary centrum (DFMMh/FV 732).

Whereas several morphological changes are observed through the cervicodorsal transition and the first dorsal vertebra, the posterior part of the trunk is more conservative in its morphology, and thus it is more difficult to infer the position of isolated elements. The description of the posterior dorsal vertebrae is mainly based on the two complete mature elements (DFMMh/FV 712.1 and 652.4; Figs 21, 22).

The posterior dorsal centra are more elongated than the centra of anterior and middle dorsal vertebrae. The ratio of the anteroposterior length divided by the posterior width of these centra is close to 1.5 (Online Supplementary Material). Therefore, posterior dorsal centra are relatively longer than the preceding dorsal centra. The centra are opisthocoelous but, in contrast to the preceding presacral elements, the anterior convexity does not occupy the entire anterior side of the centrum. Instead, it is restricted to two-thirds of the dorsal aspect of the centra, especially in DFMMh/FV 652.4 (Fig. 22B), a difference interpreted as resulting from a more posterior position of this element, as the anterior convexity decreases posteriorly in other basal camarasauromorphs (e.g. *Haplocanthosaurus*, CM 572; *Camarasaurus*, see Osborn & Mook 1921; *Tehuelchesaurus*, MPEF-PV 1125). The pleurocoels are present and well defined in the two complete elements (DFMMh/FV 652.4 and 712.1; Figs 21B, 22B). The pleurocoels of these vertebrae are anteriorly wide and posteriorly acute, but lack the internal expansion observed in anterior and middle dorsal vertebrae. Instead, the pleurocoels do not open into internal camerae as observed in the preceding dorsal vertebrae, and therefore the most posterior dorsal vertebrae of *Europasaurus* are not camerate. Therefore, *Europasaurus* differs from other basal camarasauromorphs such as *Camarasaurus* and especially *Brachiosaurus* in which internal camerae are present throughout the dorsal sequence (FMNH 25107).

The parapophysis is situated well above the centrum, and is as high as it is wide in one of the elements (DFMMh/FV 712.1; Fig. 21B), but almost twice as high as it is wide in the other vertebra (DFMMh/FV 652.4; Fig. 22B). This difference is interpreted as resulting from the more anterior position of DFMMh/FV 712.1 as a similar shape in the parapophysis is observed in middle dorsal

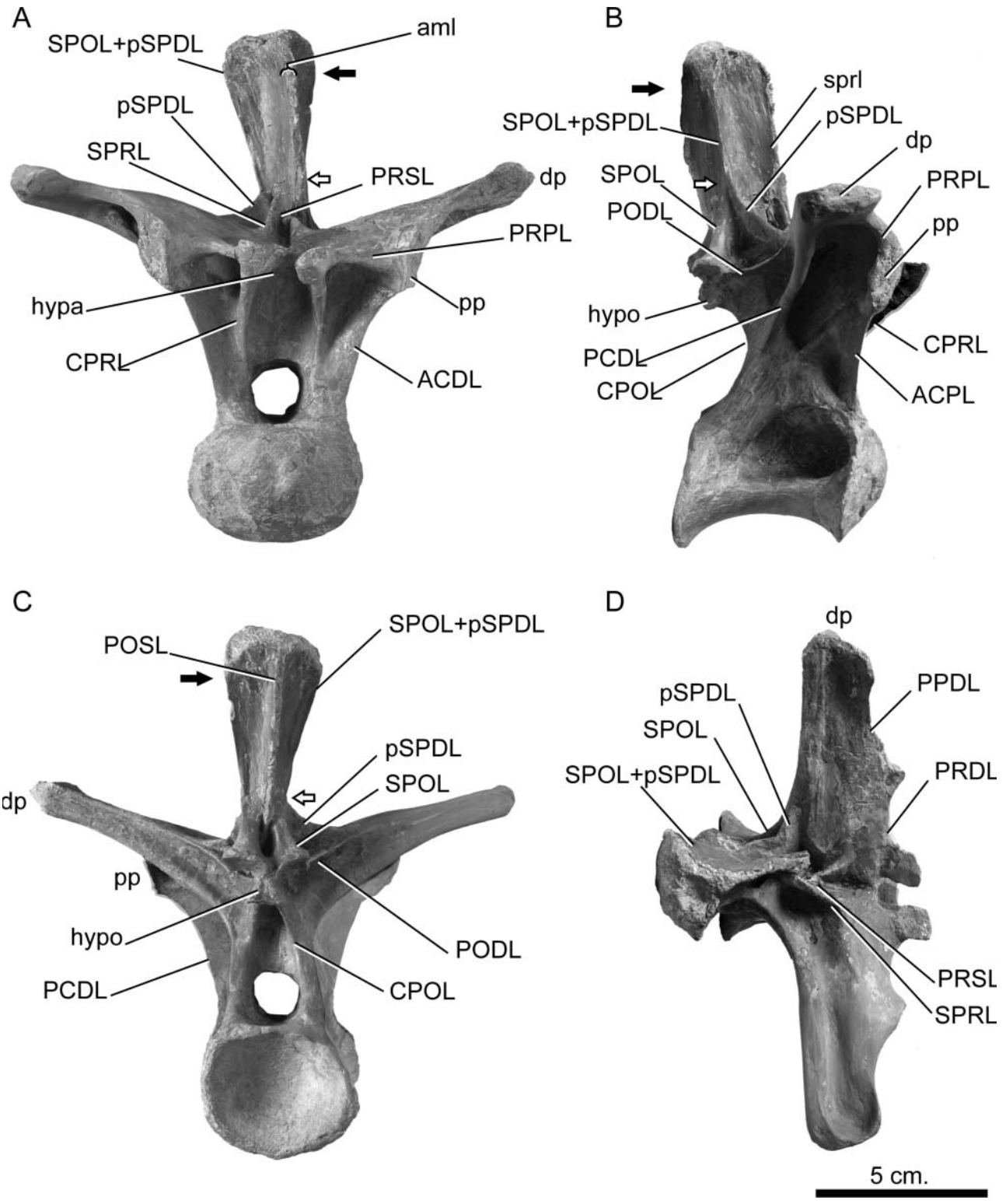

Figure 21. *Europasaurus holgeri*, posterior dorsal vertebra (DFMMh/FV 712.1) in **A,** anterior, **B,** lateral, **C,** posterior and **D,** dorsal views. The solid black arrow shows the position of the triangular aliform process and the unfilled white arrow with black border shows the point of junction of SPOL and pSPDL. See text for abbreviations.

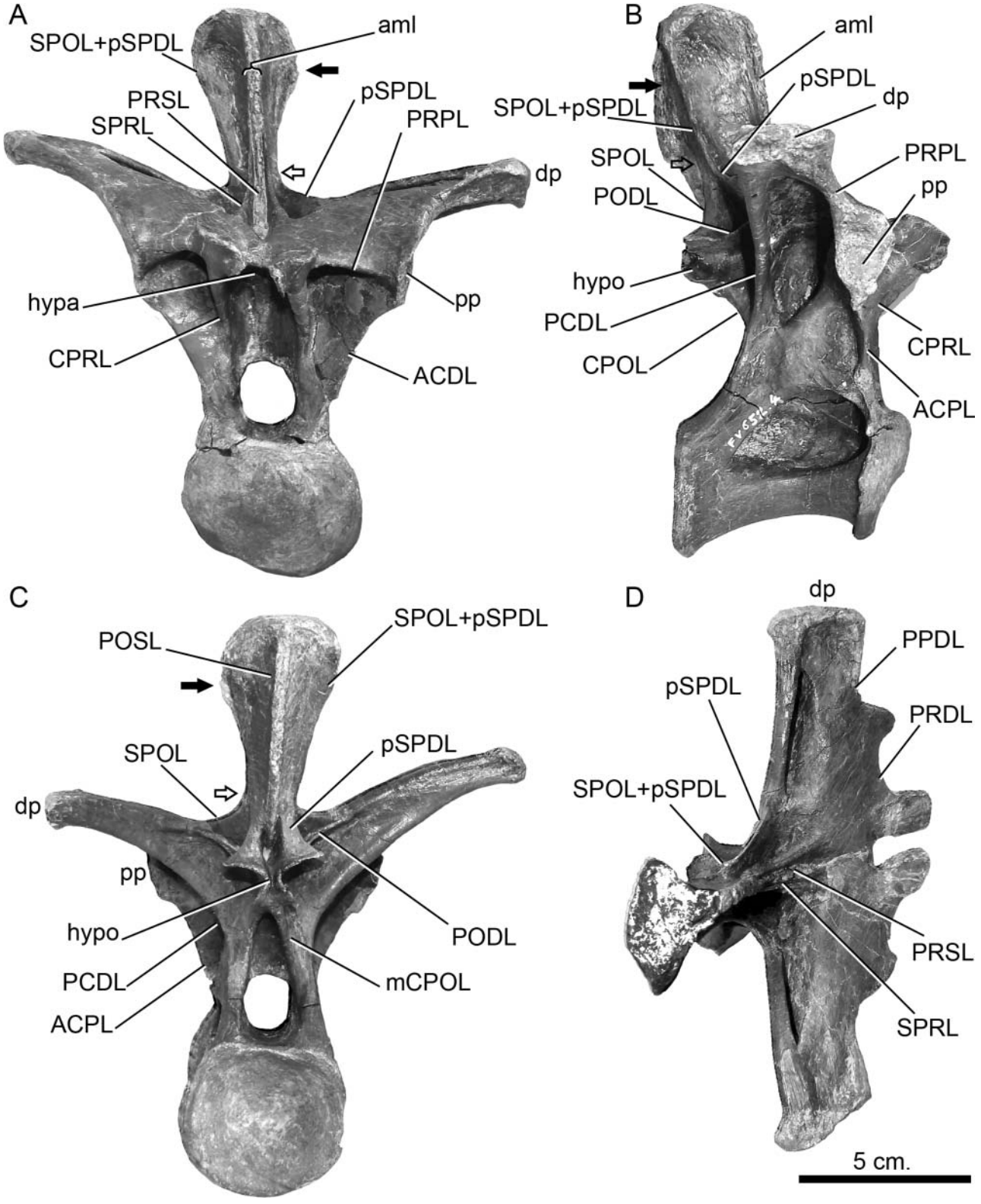

Figure 22. *Europasaurus holgeri*, posterior dorsal vertebra (DFMMh/FV 652.4) in **A,** anterior, **B,** lateral, **C,** posterior and **D,** dorsal views. The solid black arrow shows the position of the triangular aliform process and the unfiled white arrow with black border shows the point of junction of SPOL and pSPDL. See text for abbreviations.

vertebrae. The CPRL extends from the ventral margin of the prezygapophysis down to the centrum, delimiting a fossa that encloses the neural canal (the CPRF; Figs 21A, 22A). A narrow and dorsally directed lamina (the ACPL) links the ventral margin of the parapophysis with the anterior aspect of the centrum, just above the beginning of the anterior articular surface (Figs 21B, 22B). As the parapophysis becomes higher in posterior dorsal elements, the PRDL is interrupted and thus not present in posterior dorsal vertebrae of *Europasaurus*. Therefore, the horizontal lamina of Osborn & Mook (1921), usually formed by the PRDL and the PODL (Wilson 1999), is formed by the PRPL, the PPDL and the PODL. This unusual arrangement of laminae (Wilson 1999) does not represent an autapomorphic character of *Europasaurus* as it is observed in other sauropods (e.g. *Brachiosaurus*; FMNH P 25107). A composite lamina (PODL–pSPDL) extends along the posterodorsal aspect of the transverse process, from the diapophysis to the base of the neural spine. At this point the lamina splits into the pSPDL and the PODL, which is always less developed than the pSPDL (Figs 21B, C, 22B, C). The PODL extends from the split down to the ventral margin of the hyposphene (Figs 21B, 22B). A mediolaterally long fossa, which is present on the dorsal surface of the transverse process, is posteriorly enclosed by this composite lamina (PODL–pSPDL; Figs 21D, 22D). This fossa is also present in the preceding dorsal vertebra of mature elements. No PCPL is present in any dorsal vertebrae, differing from the condition widely distributed among titanosauriforms (e.g. *Euhelopus*, PMU 233; *Brachiosaurus*, FMNH 25107).

The transverse process is slightly oriented dorsally and supported posteroventrally by the PCDL. As in middle dorsal vertebrae, the PCDL is a narrow lamina that does not have any ventral expansion or bifurcation (Figs 21B, 22B), which is widely distributed among somphospondylians sauropods (Salgado *et al.* 1997). Resulting from the arrangement in the parapophyseal laminae of *Europasaurus*, the CDF and PRCDF are quite different to those observed in anterior and middle dorsal vertebrae. As in the anterior vertebrae, the PCDL forms the posterior edge of the CDF. The PRCDF is bounded anteriorly by the CPRL, instead of the PRPL as in the middle dorsal elements. Because of the absence of the PRDL in posterior dorsal vertebrae, the PRPL forms the dorsal margin of this anterior infradiapophyseal fossa, whereas the ACPL bounds this fossa posteroventrally (Figs 21B, 22B).

The prezygapophyses are almost flat and less inclined than in the preceding dorsal vertebrae, forming an angle of 20° to the horizontal. The prezygapophysis is supported ventrally by a thin CPRL. The CPRL, which is absent in middle dorsal and posteriormost anterodorsal vertebrae, links the prezygapophysis with the anterior aspect of the centrum (Figs 21A, 22A). In anterior view, both CPRL delimit a deep single CPRF, which bounds the neural canal. The mCPOL is well developed, dorsally contacting the lateroventral margin of the hyposphene and ventrally connecting to the posterolateral edge of the centrum (Figs 21C, 22C).

In anterior view, the neural spine is petal-shaped, being around 30% lateromedially wider than anteroposteriorly long. As in other non-titanosauriform sauropods, the neural spine is oriented dorsally as opposed to posterodorsally as in *Brachiosaurus* FMNH 25107 and more derived sauropods. The anterior part of the neural spine is formed by the paired SPRL and the single PRSL, which together form the anterior median lamina (Figs 21A, 22A). The PRSL can be recognized as a thin, anteriorly projected lamina. Whereas on the ventral third of the neural spine the SPRL and PRSL can be clearly distinguished from each other, dorsally the two laminae are fused to form the anterior median lamina (Figs 21A, 22A). The SPRLs diminish on the lateral edge of the median lamina, and thus probably only slightly contribute to the dorsal end of it. The pSPDL is directed posterodorsally from its ventral point of origin in the transverse process and dorsally contacts the SPOL. The SPOL extends dorsally from the middle dorsal edge of the postzygapophysis up to its contact with the pSPDL. A composite lamina (SPOL + pSPDL) forms the triangular aliform process (Upchurch 1998; Upchurch *et al.* 2004), which is located well above the junction of the pSPDL and the SPOL (Figs 21, 22). The posterior aspect of the neural spine is mainly formed by the single POSL, which runs from the deep and small SPOF up to the dorsal margin of the neural spine. The shape and size of the POSL are equal to those of the PRSL, which forms the median lamina in anterior view. Therefore, as in the preceding dorsal vertebrae, both laminae (POSL and PRSL) are similar in shape and size.

Immature dorsal centra. Among the preserved centra (Fig. 23), two developmental stages can be differentiated. The more immature centrum (DFMMh/FV 714; Fig. 23A) is around half the size of the largest immature element and is only slightly excavated on its lateral side. Therefore, the pleurocoel is regarded as absent in this element. The shallow excavation is smooth except for the anterodorsal corner, which is vascularized. A more mature stage can be recognized in DFMMh/FV 568 (Fig. 23B) in which the lateral surface is well excavated and the pleurocoel can be recognized. This pleurocoel does not open to internal camerae. Because it cannot be absolutely known if this element is part of a middle dorsal vertebra (in which internal camerae are present) or a posterior dorsal vertebra (in which no internal camerae are observed), it is not possible to know whether the element represents an advanced ontogenetic stage (if it is a posterior dorsal element) or is still far from maturity (if it is a middle dorsal). The pleurocoel of this element is extremely vascularized on the entire internal surface, indicating fast remodelling of the bone.

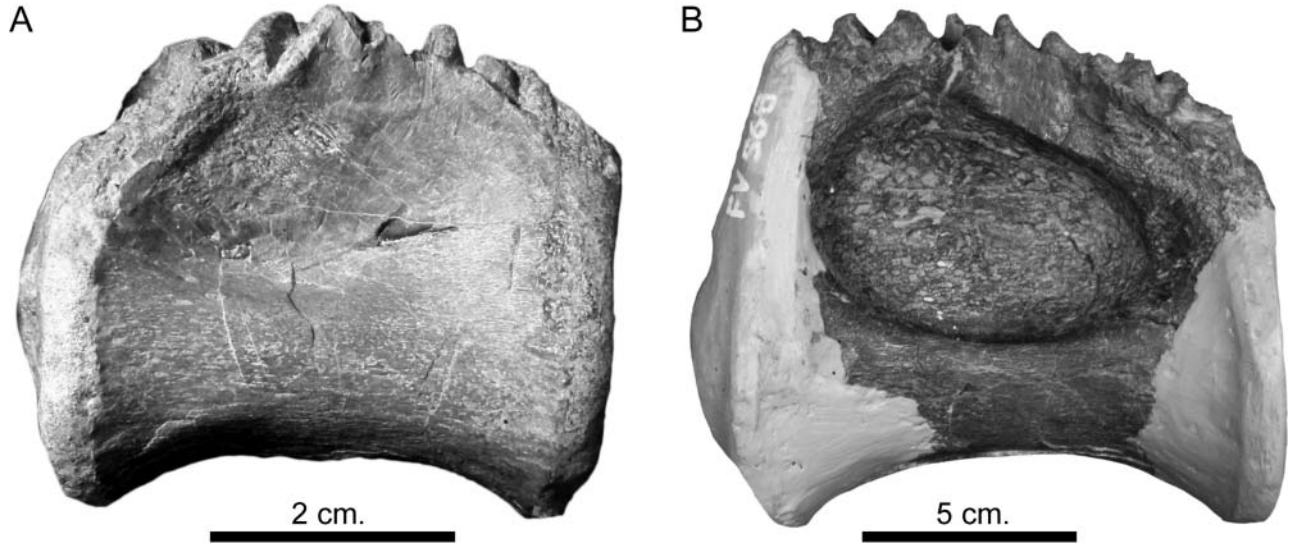

Figure 23. *Europasaurus holgeri*, immature dorsal centra in lateral view. **A,** DFMMh/FV 714; **B,** DFMMh/FV 568.

Sacral vertebrae

Only one complete sacrum is known for *Europasaurus*, but this was destroyed during a fire in 2003 (DFMMh/FV 100), as well as the second partially preserved sacrum, composed of a fourth sacral vertebrae, which was illustrated by Sander *et al.* (2006, supplementary fig. 2C; DFMMh/FV 082) (Figs 24, 25). Element DFMMh/FV 100 was articulated, with a complete sequence of 13 caudal vertebrae (Fig. 24). In addition to these specimens, several immature sacral elements are preserved, which include two articulated sacral vertebrae with their sacral ribs disarticulated (DFMMh/FV 890.5, DFMMh/FV 890.3 and DFMMh/FV 890.4), isolated sacral centra (e.g. DFMMh/FV 569), sacral ribs (e.g. DFMMh/FV 565.3, 890.7, 834.4, 553.2) and neural arches (DFMMh/FV 862, 20, 875.2). The following description is based on pictures of the complete sacrum, with more detailed comments on immature elements, to which we had direct access. It is not currently possible to describe in detail the ontogenetic changes in this section of the vertebral column as no complete mature elements have been studied.

The identification of sacral structures is made possible by the presence of several immature elements. Despite the fact that the adult sacrum of sauropods does not preserve the morphological pattern of presacral vertebrae (Wilson 2011), several laminae and fossae can be identified in the immature sacral elements of *Europasaurus*. Therefore, we interpret this 'lack' of morphology in mature specimens as a product of the bone remodelling through sacralization.

Despite its small size, the sacrum of *Europasaurus* is composed of five sacral vertebrae (Fig. 24), a condition widely distributed among non-somphospondylian neosauropods (e.g. Salgado *et al.* 1997; Wilson 2002). This information is based on the most complete specimen (DFMMh/FV 100), which probably represents a late juvenile or a subadult animal, as some of its sacral vertebrae are fused, as are the sacral ribs to the vertebrae. Nevertheless, the caudal vertebrae are regarded as immature, as at least some have open neurocentral sutures (see caudal 4 in Fig. 24A, C). Based on recent information (e.g. Wilson & Sereno 1998; Pol *et al.* 2011; but see McIntosh *et al*. 1996 and Carballido *et al*. 2011b), we interpret sacral vertebrae 2, 3 and 4 of DFMMh/FV 100 as the two primordial (S3 and S4) plus the first dorsosacral vertebra added in basal sauropodomorphs (S2). Therefore, the elements S2 to S4 form the 'primary' sacrals, which are present in sauropodomorphs more basal than *Leonerasaurus*, *Plateosaurus* being the only exception (Pol *et al*. 2011). The fifth sacral vertebra, judging from the pictures, seems to be fused in some way to the 'primary' sacrals and is assigned to a caudosacral vertebra, whereas the first sacral, completely free, is assigned to a dorsosacral. Therefore, based on the degree of fusion, specimen DFMMh/FV 100 seems to follow the sacralization model proposed by previous authors (e.g. Wilson & Sereno 1998; Pol *et al.* 2011), in which the last vertebrae incorporated into the sacrum is the dorsosacral, both during evolution and ontogeny. No fusion scar between the sacral ribs and sacral vertebrae was detected in this specimen, indicating that the ribs are strongly fused with the vertebrae. Additionally, the 'sacricostal yoke', present in DFMMh/FV 082, whose presence is a synapomorphy of *Barapasaurus* and more derived sauropods (e.g. Wilson 2002; Allain & Aquesbi 2008), is not present in DFMMh/FV 100, an absence interpreted as due to the ontogenetic stage of this specimen.

In early juvenile sauropods, the sacrum seems to be composed of fewer vertebrae (i.e. fewer vertebrae articulate with the ilium), as was recently described for the early

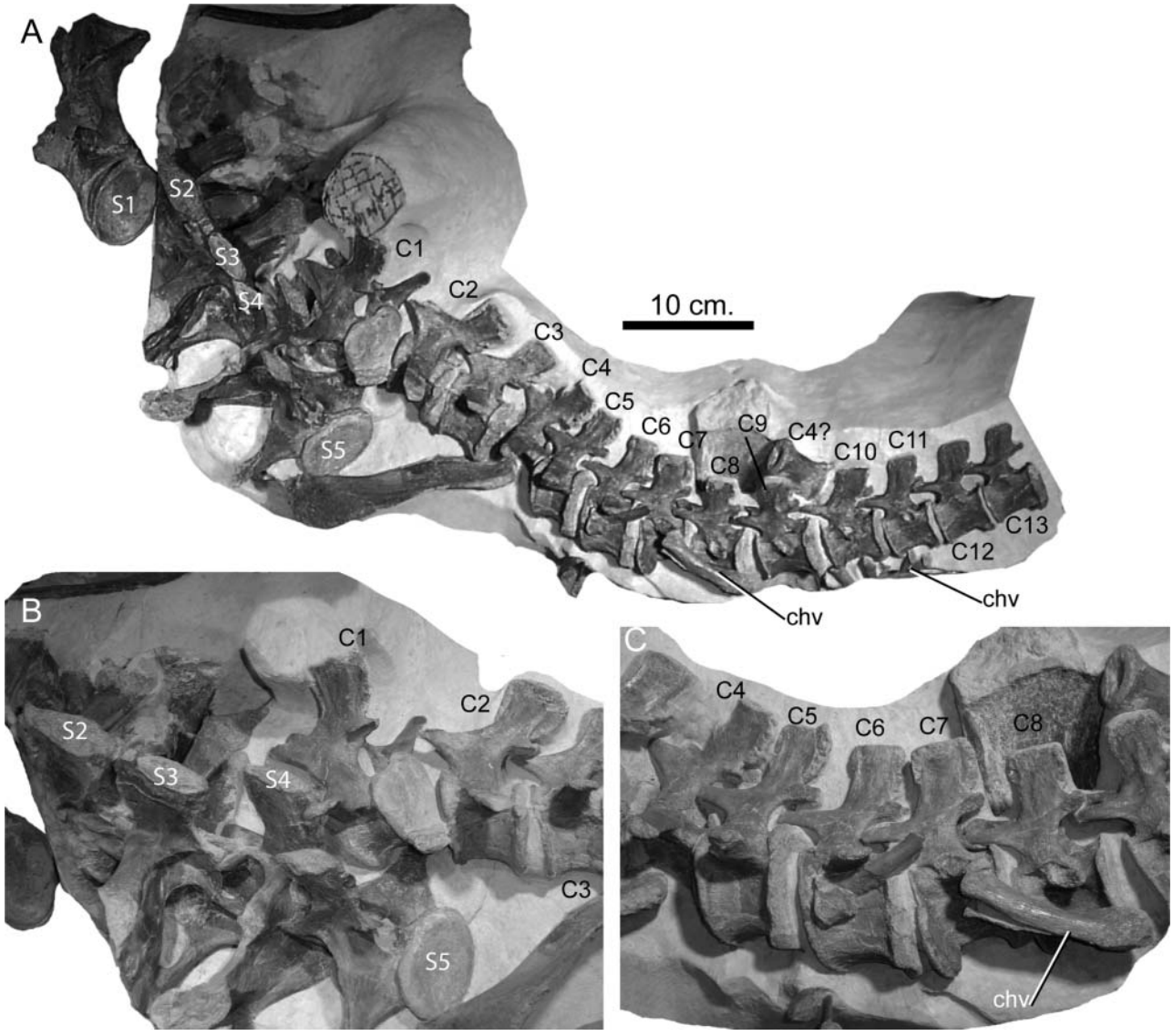

Figure 24. *Europasaurus holgeri*, DFMMh/FV 100, composed of five sacral vertebrae and the anteriormost 13 caudal vertebrae. **A,** overview; **B,** second to fifth sacral vertebrae; **C,** fourth to eighth caudal vertebrae with chevrons close by but not in position.

juvenile sauropod from the Morrison Formation (SMA 0009; Carballido *et al.* 2012a). The other sacrum, illustrated by Sander *et al.* (2006) is composed of four sacral vertebrae (DFMMh/FV 082; Fig. 25A, B). The anterior surface of the first preserved vertebra is slightly convex, and is recognized as the second sacral, the first dorsosacral to be incorporated into the sacrum, following the sequence of sacralization proposed by Wilson & Sereno (1998) and Pol *et al.* (2011). Therefore, we suggest that the first sacral was still not fused to this sacrum, and should be a dorsosacral. Whereas the second sacral has a convex anterior articular surface, the posterior articular surface of the fifth sacral (the posteriormost preserved) is flat to slightly concave. The distal ends of the sacral ribs of these two elements are fused laterally, forming the sacricostal yoke (Fig. 25A).

The two fused sacral vertebrae of the partially preserved sacrum (DFMMh/FV 890.5) are regarded here as the two primordial sacral elements (S3 and S4; Fig. 25C–E). The prezygapophysis of the fourth sacral can be recognized on the lateral aspect of this specimen, indicating low osseous remodelling, and also an early ontogenetic stage. The neural arches are well fused to the centra, whereas the sacral ribs are disarticulated. The articulation surfaces of the ribs show a wrinkled scar pattern, similar to that observed in the neurocentral articulation of the anatomically immature individuals. The sacral ribs articulate mostly ventrally with

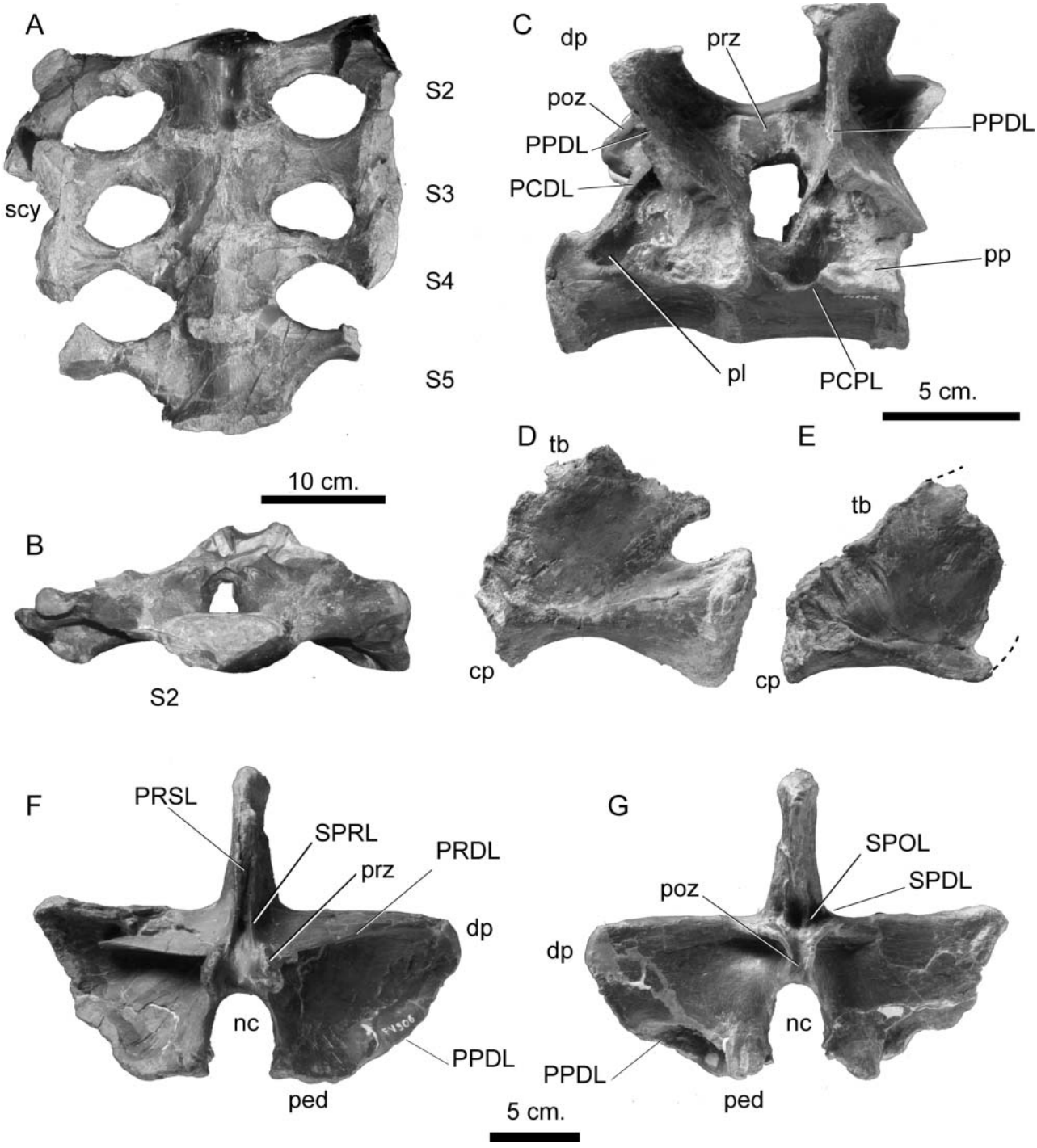

Figure 25. *Europasaurus holgeri*, sacral vertebrae. **A, B,** DFMMh/FV 082 in **A,** ventral and **B,** anterior views. **C,** DFMMh/FV 890.5, lateral view. **D,** DFMMh/FV 890.3, its sacral ribs. **E,** DFMMh/FV 890.4, anterior view. **F, G,** DFMMh/FV 906, immature sacral neural arch in **F,** anterior and **G,** posterior views. See text for abbreviations.

a V-shaped articulation. The V-shaped articulation for the ribs is in the anterior half of the centrum and this articulation continues dorsally, becoming a thin laminar articular surface that seems to end in the lateromedial aspect of the transverse process (Fig. 25C). Thus, we interpret that most of the articulation of the sacral ribs is on the parapophysis and continues through the PPDL (see below) and that the diapophysis articulates minimally with the

tuberculum, which is virtually absent. One lamina contacts the ventral articulation for the sacral ribs (here identified as the parapophysis) to the centrum; thus, this lamina is recognized as the PCPL (Fig. 25). From the parapophysis, a laminar articular surface runs up to the dorsal aspect of the vertebrae. This lamina is oriented posterodorsally in its ventral half, becoming directed laterodorsally in its dorsal half and contacting the transverse process ventrally. We interpret this lamina as the PPDL. Another lamina extends anterodorsally from the posterior aspect of the centra and contacts the PPDL at half of its height. This lamina should be the ACDL. The PPDL forms, especially in its ventral half, the dorsal articulation of the sacral rib. The PRCDF is well developed and bounded by the PPDL and ACDL, as in posterior dorsal vertebrae. This fossa mainly projects dorsally in sacral vertebrae. The CPRL and CPOL are also present.

The neural spine of an isolated neural arch is formed by the paired SPRL, SPOL and also the SPDL (DFMMh/FV 906; Fig. 25F, G). No SPDL can be recognized in the pictures of the DFMMh/FV 100 specimen. The morphology of the first two neural spines cannot be known because only the neural spines of the last three vertebrae were preserved before the fire. The SPDL of this element dorsally contacts the SPOL, forming a composed lamina, which seems not to be expanded laterally as was the composed lateral lamina of dorsal vertebrae, and therefore the triangular aliform process is not present. Nevertheless, as this is an isolated and indeed immature element, it cannot be known if its morphology is just a product of the early ontogenetic stage or the real adult morphology of the first sacral neural spines. The three posterior sacral vertebrae of DFMMh/FV 100 are simpler than this neural spine, and therefore more similar to the morphology observed in caudal vertebrae.

Caudal vertebrae

Despite caudal vertebrae being some of the most conspicuous elements to be found in the fossil record, this part of the axial skeleton is least represented among the material of *Europasaurus*. Although specimen DFMMh/FV 100 preserves an articulated sequence of 13 caudal vertebrae, further preparation is needed for a detailed description. This is because the specimen was damaged by fire, and we have to rely on pictures. Together with some isolated caudals (see Online Supplementary Material), these form the basis of the description. Additionally, no information about ontogenetic changes can be provided for caudals, as no morphological differences were observed among the elements preserved, apart from the neurocentral suture and disarticulation of the transverse processes.

Anterior caudal vertebrae. In addition to specimen DFFMh/FV 100, several caudal elements (Figs 24, 26) were recovered that include juvenile isolated centra (DFFMh/FV 132, 716, 717) and neural arches (DFMMh/FV 240, 782), as well as mature caudals (DFMMh/FV 133, 134, 495.3, 884, 743, 775). Anterior caudal vertebrae are identified as those with a low ratio (<1) of total anteroposterior length divided by the average ventrodorsal height and lateromedial width. Measurements for specimen DFMMh/FV 100 were taken from pictures and therefore are less reliable. Besides the lower ratio, anterior caudal vertebrae show well-developed transverse processes. Based on this change in the morphology, the anteriormost 11 caudal vertebrae of specimen DFMMh/FV are regarded as anterior caudals (despite the slightly higher ratio obtained for the 10th and 11th caudal of this specimen).

Among the isolated caudals, DFMMh/FV (Fig. 26) is one of the most complete elements. Anterior caudal centra are slightly concave at both anterior and posterior articular surfaces, showing the plesiomorphic state for Neosauropoda (amphicoelous anterior caudal vertebrae). Ventrally, the centra are slightly convex transversely, but the anteriormost vertebrae are almost flat or only slightly excavated. The lateral surfaces of the centra are smooth, without any trace of lateral excavation or lateral ridges. The transverse process is dorsoventrally flat and posteriorly curved, slightly surpassing the posterior articular surface. A similar orientation of the caudal transverse processes is present in several titanosauriforms (Mannion & Calvo 2011). Therefore, its presence in *Europasaurus* could indicate a more widespread distribution among macronarian sauropods. No diapophyseal lamina can be recognized, and it is thus regarded as absent in *Europasaurus*. Although the absence of well-developed diapophyseal laminae is a widespread character among non-diplodocid sauropods (e.g. Wilson 2002; Whitlock 2011; Mannion *et al.* 2012), diapophyseal laminae are well developed in many rebbachisaurid diplodocoids (Mannion *et al.* 2011a).

In specimen DFMMh/FV 100, the transverse processes are well developed throughout the anteriormost 10th or 11th vertebrae, but are short from the sixth caudal and extremely reduced in the last preserved caudal vertebrae (regarded here as middle caudals). The neural arch is short, with low zygapophyses, and with a total height of less than or equal to the centrum height (Fig. 26). The neural arch is anteriorly positioned in the centrum, a widespread character among titanosauriforms (Salgado *et al.* 1997) and closely related forms (e.g. *Tastavinsaurus*; Canudo *et al.* 2008). The prezygapophyses slightly surpass the anterior articular surface, and the postzygapophyses does not show any signs of a hyposphene ridge, which is regarded as absent, a synapomorphy of Rebbachisauridae (Mannion *et al.* 2012) and Titanosauria (Upchurch *et al.* 2004; and present analysis). The neural spine is posterodorsally directed, forming an angle of around 70° with the vertebral long axis. In *Europasaurus*, the neural spine is lateromedially compressed, being around six times longer than wide. A smooth but well discernible SPRL forms the anterior edge of the neural spine laterally from the

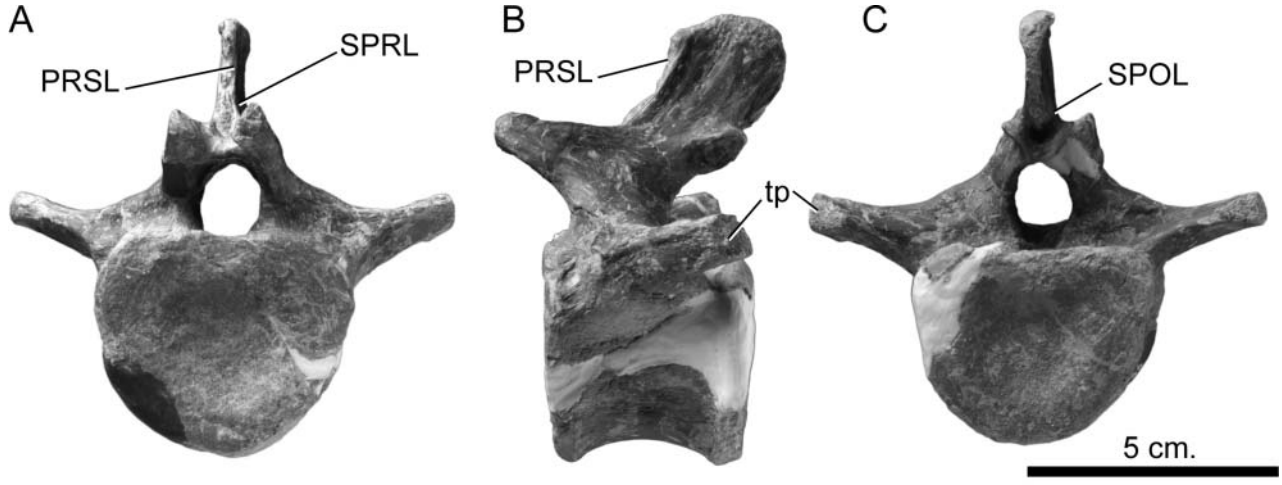

Figure 26. *Europasaurus holgeri*, anterior caudal vertebrae (DFMMh/FV 866) in **A,** anterior, **B,** lateral and **C,** posterior views. See text for abbreviations.

prezygapophyses, as in other macronarians (e.g. *Giraffatitan*; HNM SII). These SPRL do not project laterally, which contrasts with the condition that is widespread in diplodocoids (Whitlock 2011). Despite this, both SPRL (left and right) closely extend onto the anterior face of the neural spine, where a rough and low PRSL is observed.

Middle caudal vertebrae. Middle caudal vertebrae (Figs 24, 27) are represented by the last caudals preserved in specimen DFMMh/FV 100, which include isolated juvenile centra (DFMh/FV 837.2) and neural arches (DFMMh/FV 286, 716, 718), and mature elements (DFMMh/FV 546, 553.1, 700.2, 558.3, 781, 719, 180). As noted above, middle caudal vertebrae are distinguished from anterior caudal vertebrae by their higher ratio of anteroposterior length to the average of lateromedial width and dorsoventral height of the posterior articular surface. Anterior middle caudal vertebrae have weakly developed transverse processes and facets for the chevron articulation, which are easily distinguished in posterior view (Fig. 27D). As for the anterior caudal vertebrae, the middle caudal centra are amphicoelous without lateral excavations. The ventral surface is convex. The neural arches are anteriorly placed with the posterodorsally inclined neural spine. The prezygapophyses are long and surpass the anterior articular surface. The neural spine is anteriorly formed by both SPRL, which seem to enclose a narrow and rough PRSL (Fig. 27A).

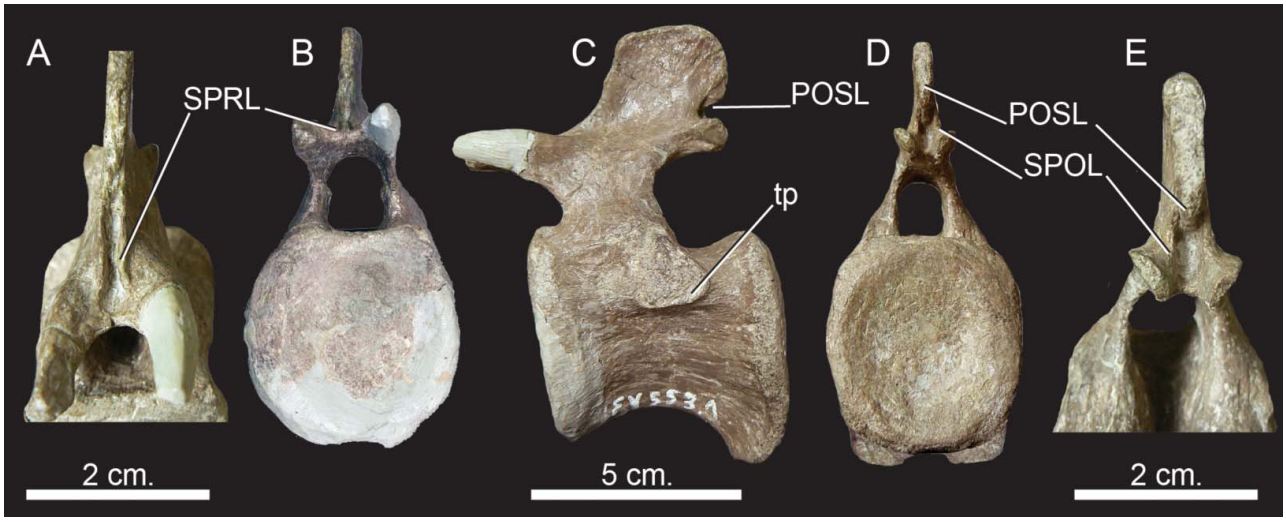

Figure 27. *Europasaurus holgeri*, middle caudal vertebrae (DFMMh/FV 553.1) in **A,** anterior view showing **B,** the details of the neural spine laminae, **C,** left lateral and **D,** posterior views with **E,** details of the neural spine in posterior view. See text for abbreviations.

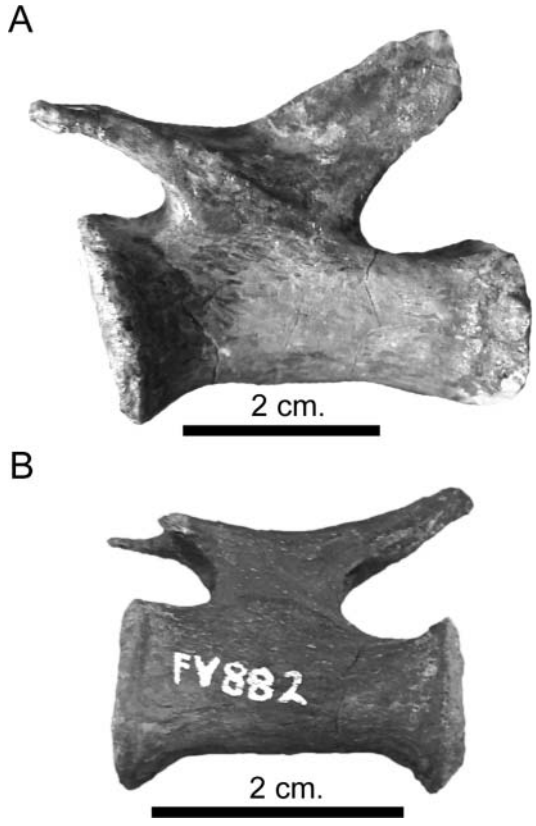

Figure 28. *Europasaurus holgeri*, posterior caudal vertebrae in left lateral view. **A,** DFMMh/FV 549.3; **B,** DFMMh/FV 882.

Posteriorly, both SPOL (left and right) can be well recognized. These laminae laterally enclose the POSL, which is rough and similar in morphology and size to the PRSL.

Posterior caudal vertebrae. Among the isolated posterior caudal vertebrae (Fig. 28), juvenile centra (DFMMh/FV 784) and neural arches (DFMMh/FV 844.4, 745), as well as mature specimens (DFMMh/FV 744, 549.2, 548, 882, 549.1, 549.3, 47 and 565.2), are represented. Posterior caudal vertebrae were identified by a higher ratio (>1.5) of centrum length compared with the average of the posterior articular surface width and height. As in other sauropods, posterior centra are relatively simple, lacking transverse processes and chevron facet articulations. The centra of posterior caudals are amphicoelous, with the neural arch anteriorly placed, although in posteriormost caudals it seems to be placed in a more medial position (DFMMh/FV 882, Fig. 28B). The ventral surface of the centra is slightly convex or almost flat. The prezygapophyses slightly surpass the anterior articular surface, and the simple neural spine is posterodorsally directed. No laminae can be identified in posterior caudals.

Cervical ribs

Several isolated cervical ribs were recovered from the quarry, but only those from specimen DFMMh/FV 838 can be unequivocally associated with its vertebrae (Fig. 9). The ribs are longer than the cervical centra, being approximately twice the centra length, a widespread character among macronarians except for *Bellusaurus* (IVPP V8299) and *Phuwiangosaurus* (Suteethorn *et al.* 2010). The ribs show differences in the angle between the capitulum and the tuberculum, as well as in the size of their process, indicating different positions in the neck, as the diapophysis becomes higher in the neural arch. Thus, some ribs can be identified as anterior cervical ribs (e.g. DFMMh/FV 469, 652.10, 652.11) and posterior cervical ribs (e.g. DFMMh/FV 544, 652.12, 834.6). In anterior cervical ribs, the capitular and tuberculum processes form a closed angle, which is smaller than 40°, but in posterior cervical ribs, the angle between these processes is a little greater than 90°. A morphological change correlates with the higher position of the diapophysis through the cervical series. A laminar connection reinforces the tuberculum and capitulum processes against one another, which is more developed in posterior cervical ribs. The capitulum is always larger than the tuberculum, especially in more anterior cervical ribs, in which the capitular articulation is twice as long anteroposteriorly as the tuberculum articulation. The capitulum is around twice as long as it is high, with an anterior rounded convexity and an anterior rounded concavity, which articulate to its counterparts in the parapophysis. In posterior cervical ribs, the anterior concavity becomes small, whereas the posterior convexity remains well developed, giving the articulation a more oval shape. The tuberculum is more or less flat and longer than it is higher in anterior cervical ribs, and rounded in posterior cervical ribs. A short triangular-shaped anterior projection is present in all of the ribs. The posterior projection, or shaft of the ribs, is long and gracile. The shaft is proximally flat, becoming rounded distally. No pneumatopore or any other pneumatic structure is present in the cervical ribs.

Dorsal ribs

Several dorsal rib elements are preserved. The description is based on the most complete elements, with well-preserved proximal ends. When these ribs are compared with those from *Giraffatitan* (Janensch 1950, figs 97–106), it is evident that most are anterior to middle dorsal ribs (e.g. DFMMh/FV 652.3, 652.9) and only some are posterior dorsal ribs (e.g. DFMMh/FV 709.1). The anterior to middle dorsal ribs are identified as those with a short capitular process and a large tuberculum process, whereas the posterior dorsal vertebra has well-developed processes, almost forming a right angle. At its proximal end, the anterodorsal ribs are anteroposteriorly flat but distally rounded through most of the rib shaft. In contrast, the shaft of the posterior dorsal ribs is anteroposteriorly flat, forming a plank-like

shape. As in the cervical ribs, no pneumatopore or internal pneumaticity is present in any of the dorsal ribs, differing from the derived condition of *Euhelopus* and titanosauriform sauropods.

Chevrons

As observed in specimen DFMMh/FV 100 (Fig. 24), the chevrons of *Europasaurus* are proximally open as in other non-flagellicaudatan neosauropods (e.g. Wilson 2002). Therefore, the chevrons are Y-shaped, straight and open (Otero *et al.* 2012). The haemal canal of the chevrons seems to be large and occupies almost half of the total chevron length, as is evident in the chevron associated with the eighth caudal vertebra. Distally, the distal process of the chevron is slightly expanded. No further morphological information is currently available for this region as only a few chevrons have been recovered.

Phylogeny

Autapomorphic characters

The complete description of the axial elements allowed us to identify two new autapomorphic characters in *Europasaurus*. Additionally, one of the supposedly autapomorphic characters previously defined (Sander *et al.* 2006) can be reinterpreted and is not included in the revised diagnosis above.

Absence of ACDL in anterior cervical vertebrae. The ACDL, as well as the other three principal diapophyseal laminae (PCDL, PRDL and PODL), is normally present in all the presacral vertebrae of sauropods (Wilson 1999). Therefore, as was noted by Wilson (1999), the absence of one or more of these laminae may be diagnostic at lower taxonomic levels. In *Europasaurus*, the absence of the ACDL precludes the presence of the PRCDF because this lamina forms the posterior edge of this fossa, distinguishing it from the CDF (Wilson *et al.* 2011). Therefore, only the CDF was identified in the anterior cervical vertebrae of *Europasaurus*. When the ACDL first appears in middle cervical elements, the PRCDF can be distinguished as well. Here we interpret the absence of the ACDL in anterior cervical vertebrae of *Europasaurus* as an autapomorphic character of this taxon.

Cervical vertebrae with pre- and postspinal laminae. Among sauropods, the presence of prespinal and postspinal laminae in posterior dorsal, sacral and caudal vertebrae is a widespread character (Wilson 1999). These two single laminae, which probably served as the attachments of interspinous ligaments, are rarely present in cervical neural arches (Wilson 1999; Salgado & Powell 2010). However, they are present in the entire cervical series of *Europasaurus*. The presence of these laminae was regarded as an autapomorphic character of *Isisaurus colberti* (Wilson 2002; Wilson & Upchurch 2003). Thus, due to the widely separated phylogenetic position of these two taxa (e.g. Sander *et al.* 2006; Carballido *et al.* 2011b), the presence of well-developed PRSL and POSL in *Europasaurus* is interpreted as an autapomorphic character of this taxon that was convergently acquired in *Isisaurus*.

Phylogenetic analysis

Europasaurus was originally recovered as a basal camarasauromorph (Sander *et al.* 2006), a position found in all three data matrices analysed by these authors (i.e. Upchurch 1998; Wilson 2002; and a modified version of Upchurch *et al.* 2004). This position was subsequently recovered in different analyses that incorporate some basal macronarian sauropods (Carballido *et al*. 2011a, b). All of these analyses place *Europasaurus* as a basal camarasauromorph. In order to further refine our understanding of the phylogenetic position of *Europasaurus* and the early evolution of macronarian sauropods, a new phylogenetic analysis was performed.

The phylogenetic analysis was carried out through a cladistic analysis using the data matrix of Carballido *et al.* (2012b), which was constructed using Mesquite V. 2.74 (Maddison & Maddison 2011) and is composed of 341 characters and 71 taxa (Online Supplementary Material). This data matrix is based on Wilson (2002), with the incorporation of previously used characters (e.g. Salgado *et al.* 1997; Upchurch *et al.* 2004; Harris 2006; González Riga *et al.* 2009; Whitlock 2011; Mannion *et al.* 2012). With respect to the data matrix of Carballido *et al.* (2011a), several forms were added, including 10 basal taxa related to the origin of Sauropoda (*Chinshakiangosaurus*, *Mussaurus*, *Antetonitrus*, *Lessemsaurus*, *Gongxianosaurus*, *Amygdalodon*, *Isanosaurus*, *Vulcanodon*, *Barapasaurus* and *Cetiosaurus*), two forms more closely related to the origin of Neosauropoda (*Turiasaurus* and *Losillasaurus*), six rebbachisaurids (*Amazonsaurus*, *Histriasaurus*, *Rayososaurus*, *Cathartesaura*, *Demandasaurus* and *Comahuesaurus*), two dicraeosaurids (*Suuwassea* and *Brachytrachelopan*), and three camarasauromorphs (*Bellusaurus*, *Cedarosaurus* and *Tapuiasaurus*). *Brachiosaurus* was split into *Brachiosaurus* and *Giraffatitan*. Of the 49 multistate characters, 24 were analysed as ordered (12, 58, 95, 96, 102, 106, 108, 115, 116, 119, 120, 154, 164, 213, 216, 232, 233, 234, 235, 256, 267, 298, 299, 301). The ordering of these characters is based on morphological similarities between the states instead of hypotheses on the evolutionary sequence of character transformation, as was also done in other phylogenetic analysis (e.g. Upchurch 1998; Upchurch *et al.* 2004).

An equally weighted parsimony analysis was carried out using TNT v.1.1 (Goloboff *et al.* 2008a, b). A heuristic tree search was performed starting from 1000 replicates of Wagner trees (with random addition sequence of taxa)

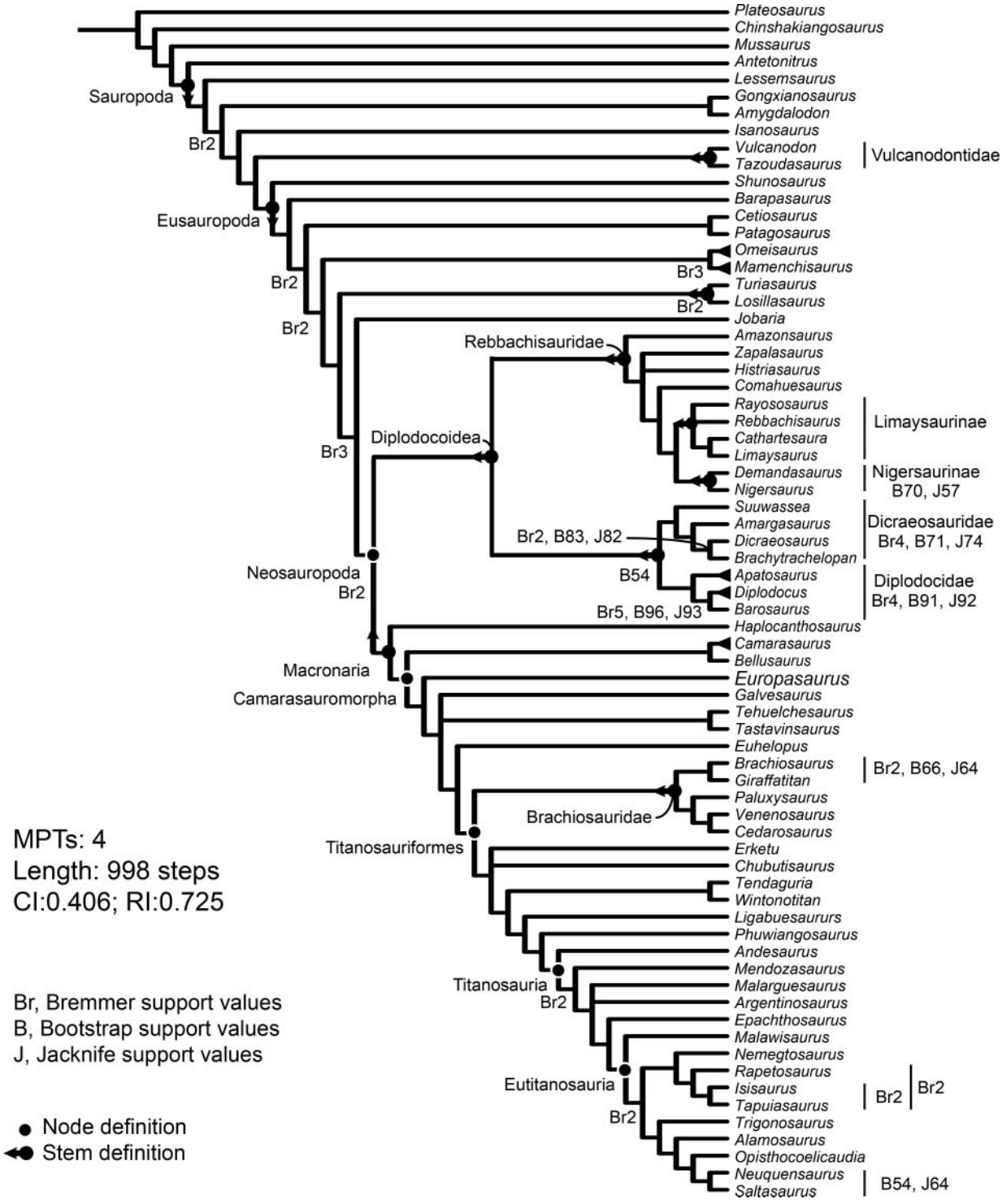

Figure 29. Strict consensus tree obtained from the 38 most parsimonious trees. Support values are indicated for each node (Bremer support index higher than 1; bootstrap and jackknife values higher than 50%).

followed by tree bisection-reconstruction (TBR) branch swapping (saving 10 trees per replicate). This procedure retrieved four most parsimonious trees (MPTs) of 998 steps (consistency index (CI) = 0.406; retention index (RI) = 0.725), found in 421 of the replicates. The strict consensus tree (Fig. 29) is almost completely resolved.

Branch support. In order to evaluate branch support, bootstrap, jackknife and Bremer support values were analysed under the TNT implemented functions. Absolute bootstrap (with standard replacement) and jackknife values (with 36% of removal probability) were calculated. The results (Bremer support higher than 2 and bootstrap and jackknife values greater than 50%) are shown in Fig. 29. The support obtained for macronarian branches is relatively low, with only a few nodes having Bremer support values higher than 1 and bootstrap and jackknife values higher than 50%. The low support may result from both missing data and/or the instability of one or more taxa (wild-cards *sensu* Nixon & Wheeler 1992) in suboptimal trees (one or more steps longer than the MPTs).

In order to evaluate the general causes of low branch support, analyses were undertaken to determine which taxa are the most unstable and their impact on the recovery of low values. For this approach, suboptimal tree searches were performed. In an initial analysis, MPTs and trees that were one step longer were searched. The tree search was performed following the same procedure described above, that is starting from 1000 Wagner trees (with random addition sequences), followed by TBR branch swapping (saving 10 trees per replicate). As a way of finding the most unstable taxa (which is the cause of the low support observed in the MPTs), the trees obtained were analysed with iterPCR (Pol & Escapa 2009). This procedure found 21 unstable taxa (Fig. 30). If these taxa are pruned from the recovered trees (MPTs and MPT + 1 step), the branches recovered have Bremer values equal to or greater than 2 (Fig. 30), and are therefore the most stable branches. In general, it was observed that the unstable taxa do not show very different positions from those recovered in the MPTs. The causes of instability are mainly the absence of information (missing data) and, in most of the taxa, a conflict in less than 5% in the characters (i.e. supporting different positions). It must be also noted that most of the unstable taxa are fairly incomplete, generally with less than 20% of the characters scored. The same procedure was applied to trees two steps longer than the MPTs. The unstable taxa identified in this second analysis are marked with a cross in Fig. 30, and these unstable taxa are more stable than the previously eliminated taxa. Once these taxa are pruned, the resulting branches have Bremer support values equal to or greater than 3. Although this procedure is extremely exploratory, it allows us to identify the most unstable zones of the tree where further efforts are needed, both in terms of taxon sampling and searching for new characters.

As a result of these analyses, two further areas of conflict (i.e. with lower support) can be identified. One is at the base of Camarasauromorpha (between *Europasaurus* and Titanosauriformes), and the other includes several basal titanosauriforms and taxa closely related to the origin of Titanosauria. As was noted by Kearney & Clark (2003), the exclusion of unstable taxa from a phylogenetic analysis will certainly result in a more 'robust' tree (with higher support values). However, the inclusion of such taxa provides a wider perspective on the evolution of Macronaria, even with the low support values observed. Low support also implies that small changes (e.g. in the coding of characters and the addition of one or more taxa) will produce topological differences.

Basal macronarian interrelationships. The results of the phylogenetic analysis are briefly described here; a complete and detailed discussion of the synapomorphies recovered and their distributions among basal macronarians can be found in the Online Supplementary Material. The analysis recovered *Europasaurus* in a basal position among camarasauromorphs, as originally suggested by Sander *et al.* (2006). *Haplocanthosaurus* was recovered at the base of Macronaria, a result that contrasts with its recent assignment to Diplodocoidea (Whitlock *et al.* 2011) but is similar to the position recovered by Upchurch (1995), Wilson & Sereno (1998) and Upchurch *et al.* (2004) (but not in the reanalysis of this matrix by Wilson & Upchurch 2009), as well as some trees in Mannion *et al.* (2012). *Tehuelchesaurus*, *Tastavinsaurus*, *Galvesaurus* and *Euhelopus* were recovered as basal camarasauromorphs, as was also suggested by Carballido *et al.* (2011a, b), although with some slight differences in their interrelationships. These differences clearly reflect the low support values obtained for Macronaria and the sensitivity of the phylogenies to taxon and character sampling. The clade Brachiosauridae is recovered in our analysis, showing for the first time fully resolved relationships.

Ontogenetic changes in the axial skeleton

Ontogenetic changes in the postcranial axial skeleton are poorly known in sauropods and most of this knowledge is based on isolated bones (e.g. Carpenter & McIntosh 1994; Foster 2005), which mainly represent late juvenile to subadult specimens (e.g. Ikejiri *et al.* 2005; Tidwell & Wilhite 2005). The identification of such changes has a great impact not only on improving our knowledge of the ontogenetic transformations in sauropods, but also on the systematic classification of early juvenile specimens. Furthermore, the improvement in knowledge of these changes could give some insights into the recognition of heterochronic processes in the evolution of sauropods.

The postcranial axial elements described above represent a range of morphological ontogenetic stages, probably from early juvenile to fully grown individuals (Sander *et al.* 2006). Most of this information is based on the presacral section, the best represented section in the *Europasaurus* material. The cervical and dorsal vertebrae of sauropods have a complex arrangement of laminae and fossae, which is of great systematic value (e.g. Bonaparte 1999; Wilson 1999; Salgado *et al.* 2006; Salgado & Powell 2010). Therefore, the morphological differences

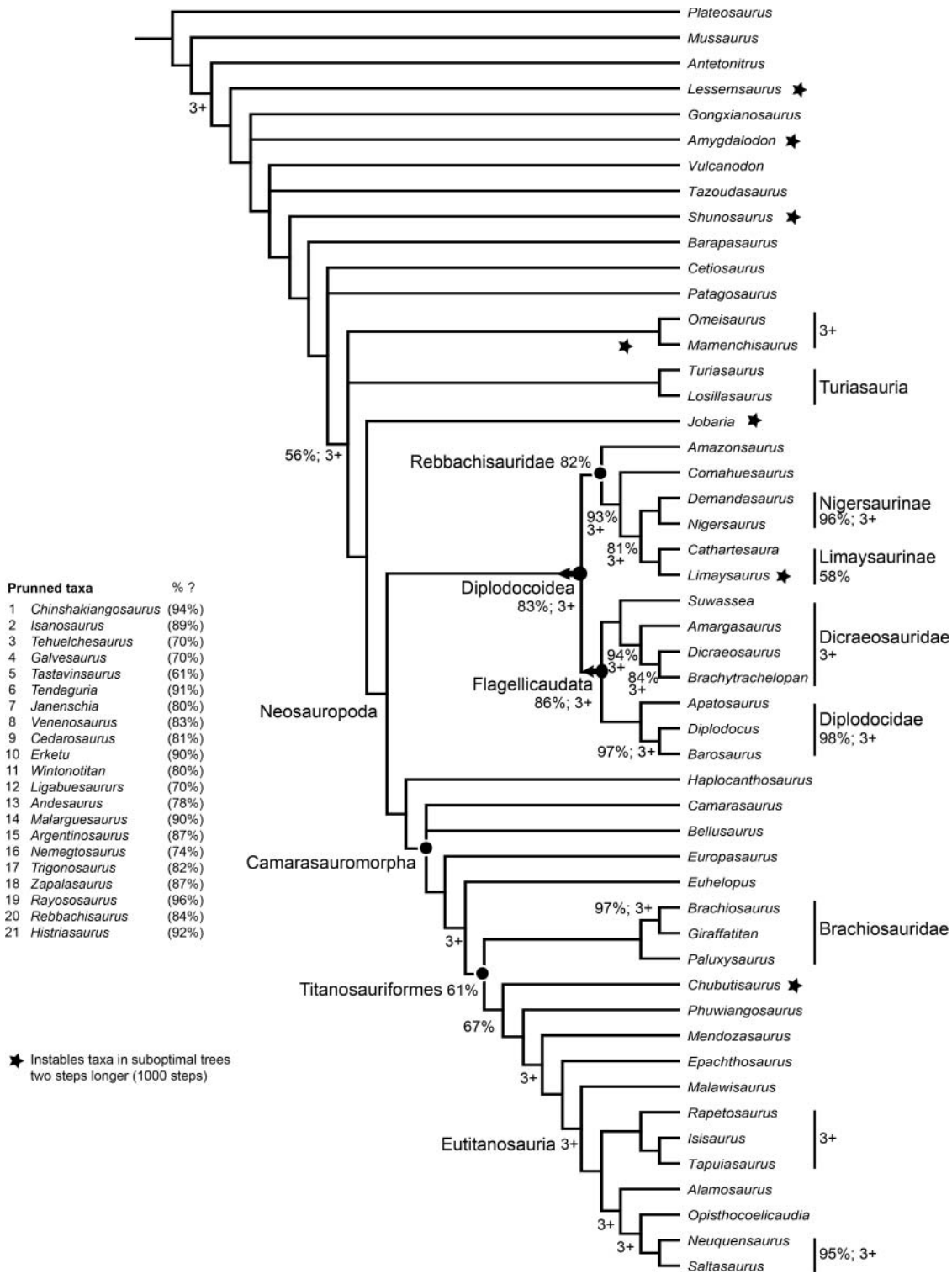

Figure 30. Strict consensus tree obtained after the pruning of more unstable taxa in suboptimal trees of one (left column) and two (star) steps longer than the MPT.

observed in *Europasaurus* provide an excellent opportunity for better understanding morphological transformations during ontogeny. Because most of the axial bones were found isolated and without unequivocal association with long bones, histology cannot be used to detect ontogenetic stage in these specimens. Although size is generally correlated with maturity (Brochu 1996), many factors influence growth rate. Indeed, identifying ontogenetic stages only with size (as was recently done by Woodruff & Fowler 2012) is ill-advised (e.g. Brinkman 1988; Brochu 1996; Irmis 2007). Consequently, the use of size-independent maturity criteria is advisable to recognize discrete ontogenetic changes (Brochu 1996).

Two easily identifiable main stages were recognized in the postcranial axial skeleton of *Europasaurus*, vertebrae with open neurocentral sutures and vertebrae with completely closed sutures. These two states were used throughout the description to differentiate immature elements (with open neurocentral sutures) from mature elements (with closed neurocentral sutures). Assessment of closure is easy in the case of *Europasaurus* because an open suture inevitably seems to have led to complete taphonomic separation of the neural arch from the centrum.

The neurocentral fusion of the last vertebra indicates that all major morphological changes had been completed and thus the specimen is morphologically mature (Brochu 1996). Full morphological maturity cannot currently be detected in *Europasaurus* because no clear pattern of suture closure is observed in Neosauropoda (Ikejiri 2003; Irmis 2007; Gallina 2011), and because no articulated specimens are known. Therefore, in this study the terms mature and immature are not directly associated with the morphological maturity of the entire specimen but rather to the morphology of isolated elements. The identification of additional size-independent morphological characters allows us to divide the mature and immature elements into further stages. A summary of these changes is provided below.

Atlas–axis complex

All atlas and axis elements were found disarticulated, and thus were identified as immature. The most significant changes in these elements are the elongation of the neurapophysis and the increasing development of the epipophysis, DFMMh/FV 632 being more immature than DFMMh/FV 791 (Fig. 1E–I). The ontogenetic elongation of the cervical vertebrae is well documented in basal sauropodomorphs (e.g. *Massospondylus*; Reisz *et al.* 2010) and neosauropods (e.g. *Camarasaurus*, SMA 0009; Ikejiri 2004; Schwarz *et al.* 2007), and therefore is to be expected in *Europasaurus*. Additionally, the axis shows that the POCDF is not present in early stages (DFMMh/FV 563.2; Fig. 2A–C) but appears before neurocentral closure as it is present in DFMMh/FV 706.1 (Fig. 2D–F). The POSL is present in the most immature element, in which the area is discernible as a postspinal scar (Fig. 2A–C). It is also present in the more mature (but still immature) element (Fig. 2D–F), thus appearing before the element matures. Because no mature atlases or axes were recovered, the immature elements cannot be compared with a completely mature atlas–axis complex.

Cervical vertebrae

Five different morphological ontogenetic stages (MOS) can be recognized among the preserved cervical vertebrae (Table 1; Fig. 31). These different ontogenetic stages are mainly based on the observations made in anterior cervical vertebrae, because this part is the best represented among the *Europasaurus* material. Three different immature stages were recognized, termed MOS 1 (early immature), MOS 2 (middle immature) and MOS 3 (late immature) (Fig. 31). Although no centra were found in association with the immature neural arches, the two are tentatively linked. Due to the slightly different development of fossae and laminae, the mature elements (with closed neurocentral suture) could also be divided into two further stages, MOS 4 (early mature) and MOS 5 (late mature).

MOS 1 (early immature). In the first stage, MOS 1, the main laminae of the neural arches (excluding the neural spine) are only slightly developed but present. The presence of neural arch laminae in early ontogenetic stages is also supported by their presence in the early juvenile sauropod SMA 0009 (Schwarz *et al.* 2007; Carballido *et al.* 2012a),

Table 1. Different morphological ontogenetic stages (MOS) of the cervical vertebrae, indicating the absence (−), weak development (− +), presence (+), and full development (++) of the most relevant characters that changes through ontogeny.

MOS	PL	CDF	SPRL	PCDF	PPLE	PRSL	NTCH
1	−+	−+	−+	−+	−	−	−
2	+	+	+	−+	−	−	−
3	+	+	+	+	+	+	−+
4	+	+	+	+	+	+	+
5	++	+	+	+	+	+	++

MOS: morphological ontogenetic stage; **PL**: pleurocoel; **CDF**: centrodiapophyseal fossa; **PCDF**: posterior centrodiapophyseal fossa; **PPLE**: fossae on the lateral surface of the prezygapophysis process; **PRSL**: prespinal lamina; **NTCH**: notch on the posterodorsal surface of the centrum.

Table 2. Morphological ontogenetic stages (MOS) of the dorsal vertebrae, indicating the absence (−), weak development (− +), presence (+), and full development (++) of the most relevant characters that change through ontogeny.

MOS	PL	NS	SPDL	PRSL	TLE	CDFPN
E–I	−	L	−+	−	−	−
M–I	−	LW	−+	−+	−	−
L–I	?	WL	+	+	+	−+
M	+	W	+	+	+	+

MOS: morphological ontogenetic stage; **NS**: neural spine shape (**L**: longer than wide; **LW**: as long as wide; **WL**: slightly wider than long; **W**: markedly wider than long); **SPDL**: spinodiapophyseal lamina; **PL**: pleurocoel; **PRSL**: prespinal lamina; **TLE**: triangular lateral expansion of the neural spine; **CDFPN**: pneumatopore in the centrodiapophyseal fossa.

which may have been only a few months old (Schwarz *et al.* 2007; Klein & Sander 2008). Most of the fossae observed in mature specimens are present in earliest ontogenetic stages as weakly developed excavations, except for the lateral excavation of the neural spine and prezygapophyseal processes, which are absent in the early stages. Whereas the paired zygapophyseal laminae (SPOL and SPRL) are present in the first immature stage, the single spinal laminae (PRSL and POSL) cannot be recognized even as low scars (DFMMh/FV 1031, 833.1). Several immature centra are included in this stage (e.g. DFMMh/FV 857.1). In these centra, the pleurocoels are only slightly developed as more or less shallow lateral excavations, which are extremely vascularized, indicating fast remodelling. The immature specimen from the Morrison Formation (SMA 009), recently suggested to be a brachiosaurid (Carballido *et al.* 2012a), shows similar development of its laminae and fossae and can be regarded as stage MOS1.

MOS 2 (middle immature). The neural arches assigned with the MOS 2 show a deep and well-developed CDF, whereas the POCDF persists as a weakly developed fossa. The paired laminae of the neural spine are better developed and clearly distinguishable. The single spinal laminae (PRSL and POSL) are not developed yet, but discernible as low scars (DFMMh/FV 119). Isolated centra in which the pleurocoels are well marked but not very deep are assigned to this stage. The surface of those pleurocoels is extremely vascularized, as is typical of fast growing tissues (Varricchio 1997).

MOS 3 (late immature). It is not until the most advanced immature stage (MOS 3) that all the fossae and laminae are well developed, even the lateral excavations present on the neural spine and on the prezygapophyseal processes (which are not identifiable in the earlier stages). The PRSL and the POSL, absent in earlier stages (or only recognized as rough surfaces), can be clearly recognized in this stage but are still not as well developed as in mature bones. The isolated cervical centra with well-developed pleurocoels and a slightly developed posterior notch are included in this stage, and show the more advanced immature morphology among the isolated centra. The surface of the pleurocoels is not as vascularized as in the preceding stage. In the MOS 3, all the morphological characters present in mature vertebrae can be easily recognized, even the autapomorphic characters of *Europasaurus*, as the PRSL and POSL. Therefore, the elements with a MOS 3, although still immature, can unequivocally be assigned to *Europasaurus holgeri*.

MOS 4 and 5 (mature cervical elements). Early mature elements (MOS 4) are recognized by their complete neurocentral closure and a slightly poorer development of the pleurocoels and posterior notch of the centrum. Internally, the pleurocoels of these centra are small areas with extremely vascularized bone surface, especially in the posterior half. Late mature cervical vertebrae (MOS 5) are differentiated from those of MOS 4 solely on the basis of more complete and deep fossae. These elements show a completely smooth bone surface in all their cavities, which is interpreted as resulting from slower growth. The posterior notch is well marked.

Dorsal vertebrae

Most of the isolated and immature dorsal vertebrae are identified as middle, or middle to posterior dorsal elements. Among immature elements three major MOS are recognized (Table 2; Fig. 31): MOS 1 (early immature), MOS 2 (middle immature) and MOS 3 (late immature) (Fig. 31). Among the preserved mature dorsals only one MOS can be identified (MOS 4; mature).

MOS 1 (early immature dorsals). In MOS 1 (early immature), all laminae of the neural arch are well developed whereas the neural arch fossae (CDF, PRCDF and POCDF) are present but not as deep as in subsequent stages. The pneumatopore of the CDF is not present in this stage. The neural spine shows two of the three paired laminae observed in mature vertebrae (SPRL and SPOL), but the pSPDL cannot be properly recognized. The single spinal laminae (PRSL and POSL) are also absent in MOS 1. Therefore, in this first MOS the neural spine remains extremely simple, resembling the plesiomorphic condition observed in basal sauropodomorphs such as *Plateosaurus* (Galton

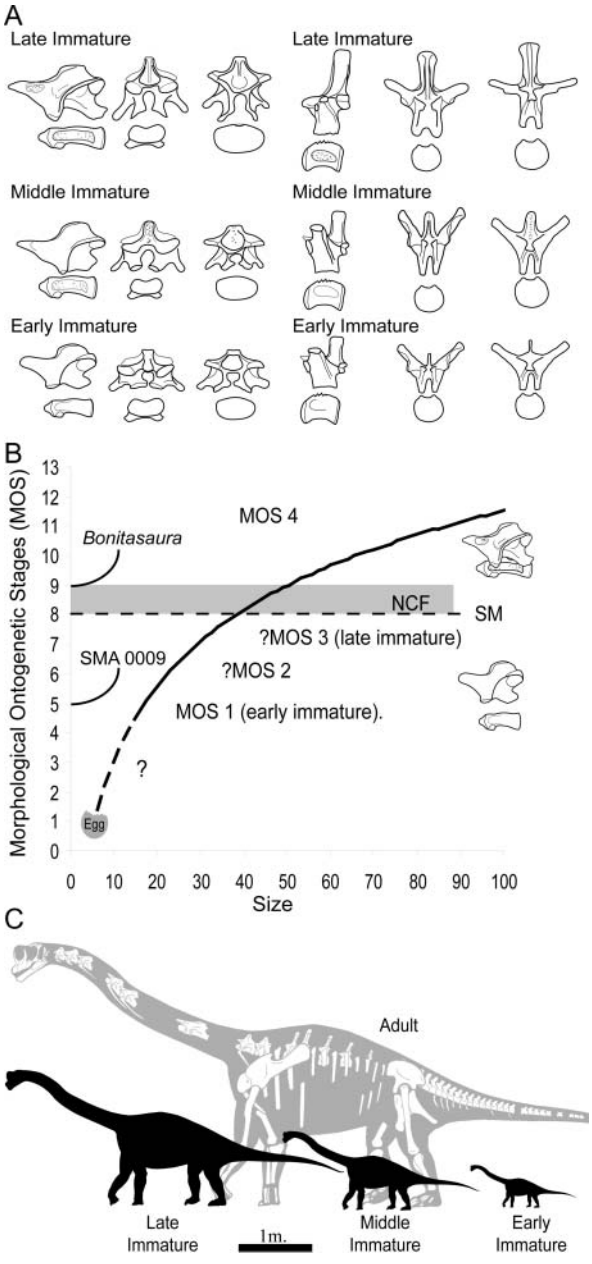

Figure 31. Major ontogenetic changes in the presacral elements of *Europasaurus holgeri*. **A,** more drastic changes observed from earliest stages to pre-mature stage (MOS1–MOS3). **B,** histological ontogenetic stages (HOS) curve showing the place in which morphological ontogenetic stages (MOS) should probably have taken place. **C,** largest adult *Europasaurus* compared with expected size of immature specimens in different ontogenetic stages (based on the largest morph of *Europasaurus*) (after *Brachiosaurus* and *Camarasaurus* reconstructions of Wilson & Sereno 1998). NCF: neurocentral fusion; SM: inferred sexual maturity time (Klein & Sander 2008).

2001), in which the spine is longer than wide. A similar neural spine was described for the juvenile specimen SMA 0009 from the Morrison Formation (Schwarz *et al.* 2007; Carballido *et al.* 2012a) and also seems to be present in juvenile *Phuwiangosaurus* vertebrae (Martin 1994). The SPDL was also described as being absent in juvenile dorsal vertebrae of the basal sauropod *Tazoudasaurus* (Allain & Aquesbi 2008). Although no dorsal centrum was associated with the neural spines of this stage, the less-developed centra described above are attributed to MOS 1. These centra are opisthocoelous and without pleurocoels or lateral fossae, as is also observed in SMA 0009 (Carballido *et al.* 2012a). The dorsal centra assigned here to MOS 1 are clearly different from the MOS 1 of cervical vertebrae in which lateral excavations are observed. This same difference was observed in the juvenile specimen from the Morrison Formation (Schwarz *et al.* 2007; Carballido *et al.* 2012a). Therefore, we interpret this as a product of a cervicodorsal trend in the ontogenetic development of internal pneumaticity, as has been described for birds, paralleling the evolutionary trend in sauropods (Wedel 2009; Carballido *et al.* 2012b).

MOS 2 (middle immature dorsals). The middle immature stage differs from the previous stage mainly in the arrangement of the neural spine laminae and the widening of the neural spine. The pSPDL is present in this MOS as a weakly developed lamina which runs close to the PODL (DFMMh/FV 243). The low neural spine is as wide as it is long. The PRSL and POSL are not present in this MOS but, contrary to MOS 1, a low postspinal and prespinal scar can be identified in this region; these are recognized as the incipient PRSL and POSL. The lateral excavations of the neural arches do not greatly differ from those of MOS 1.

MOS 3 (late immature dorsals). As for the cervical vertebrae, the MOS 3, which corresponds to the more advanced immature elements, does not differ greatly from the mature stage (MOS 4) but lacks the neurocentral suture closure. Inside the CDF, below the transverse process, a very deeply excavated area can be recognized, which is identified as the CDF pneumatopore (DFMMh/FV 857.2), but supraneural camerae are absent. In this stage, the neural spine laminae are well developed, resulting in an expanded neural spine, slightly wider than long (a synapomorphy of *Gravisauria*; Allain & Aquesbi 2008). The triangular aliform process, widely distributed among macronarian sauropods (e.g. Wilson 2002; Upchurch *et al.* 2004), can be recognized. Therefore, as with the last immature stage of the cervical vertebrae (MOS 3), all of the adult characters that carry important systematic information, but well-developed supraneural camerae, can be recognized and correctly scored in the late immature stage, though not earlier. An isolated dorsal centrum described above (DFMMh/FV 568) has well-developed pleurocoels, and therefore can be differentiated from the more immature centrum assigned to the early immature stage (MOS 1). Because it cannot be determined whether this centrum is a middle dorsal (that has internal camerae in mature specimens), or a posterior dorsal (without internal camerae

in mature specimens), it remains unknown whether the camerae formed before or after neurocentral suture closure. Nevertheless, mature internal pneumatic features seem to be developed before the closure in other neosauropods (e.g. *Alamosaurus*, *Bonitasaura*; Woodward & Lehman 2009; Gallina 2011).

MOS 4 (mature dorsals). In the single mature stage recognized all the fossae and laminae are well developed. The main difference between MOS 4 and MOS 3 is the degree of development of the laminae and fossae. For example, the CDF pneumatopore (also present in MOS 3) is more developed and penetrates deeply into the neural arch to form the supraneural camerae, which are lacking in early MOS.

Sacral vertebrae

Current knowledge on the ontogenetic changes in the formation of the sacrum, or sacralization, in *Europasaurus* is minimal as no complete adult sacrum has been observed. Nevertheless, some information related to the stages of fusion deserves to be mentioned here. Wilson (2011) adopted the interpretations of Marsh (1895) and Hatcher (1903) in which three separate units can be recognized in the sacrum – neural arch, centrum and sacral ribs – a nomenclature also followed here. The sacral elements of *Europasaurus* provide some information related to the sequence of fusion among these units, making it possible to recognize three different stages:

1. As is evident in element DFMMh/FV 890.5, the first stage is composed of two fused sacral vertebrae regarded as the primordial sacrals; the neural arch and centrum fuse with each other before fusion of the ribs and also before fusion of the two primordial sacrals with the other sacral centra. At this stage, the prezygapophysis is still distinguishable because its shape is similar to that observed in caudal vertebrae (Fig. 25).
2. A more advanced stage is recognized in DFMMh/FV 100 in which the sacral ribs are fused to the vertebrae, and sacrals two to five are also fused to some degree. At this stage, the sacricostal yoke is still not present. The presence of some open neurocentral sutures in the caudal vertebrae indicates that this stage precedes complete neurocentral closure of the caudal region (Fig. 24).
3. A third stage is observed in element DFMMh/FV 082, in which four sacral centra are fused with a fifth 'free' sacral (possibly the dorsosacral). At this stage, before fusion of the fifth sacral, the sacricostal yoke is present, at least from S2 to S4 (Fig. 25).

Sacral vertebrae homology. The homology of sacral vertebrae is far from well known. Here we follow the hypothesis recently proposed by Wilson & Sereno (1998) and Müller *et al.* (2010) in which a dorsosacral is first added to the two primordial sacral vertebrae, forming the three primordial sacral vertebrae of sauropodomorphs, into which a caudosacral and an additional dorsosacral vertebrae are incorporated. Nevertheless, at least a few examples do not seem to follow this pattern (e.g. McIntosh *et al.* 1996; Carballido *et al.* 2011b). The addition of vertebral elements to a section of the trunk (e.g. cervical, dorsal and sacral) can take place by two main processes: addition of new elements, or incorporation of elements of adjacent sections (e.g. dorsal vertebrae are incorporated into the neck, or caudal and dorsal vertebrae are incorporated into the sacrum). The hypothesis of Wilson & Sereno (1998) and Müller *et al.* (2010) only takes into account the second process (incorporation), whereas addition is not considered.

Whereas basal synapsids share a conservative axial configuration, reptiles show plasticity in axial developmental, a product of both homeotic regionalization and somitogenesis (Müller *et al.* 2010). Differences in the speed of the 'segmentation clock' (molecular oscillator), which controls somitogenesis, result in a variable number of vertebrae (see Müller *et al.* 2010). Addition of presacral vertebrae is well known in the evolution of sauropods (Wilson & Sereno 1998). Whereas the plesiomorphic number of presacral vertebrae for sauropodomorphs is regarded as 24, *Shunosaurus* has 26 and *Omeisaurus* 28, indicating the formation of new elements (addition), a process that can be suggested for other sauropods (e.g. *Euhelopus*, *Futalongkosaurus*; Wilson & Upchurch 2009; Calvo *et al.* 2007). Therefore, somitogenesis could also alter the number of sacral vertebrae (as it does for presacral and caudal elements), and the incorporation of dorsal and caudal vertebrae would not be the only explanation for an increment increase in sacral elements. Although difficult to observe in fossil record (as also is incorporation), the possible addition of sacral vertebrae via somitogenesis should be taken into account, especially when elements are being homologized.

MOS, systematic and evolutionary implications

In order to test the phylogenetic signal of the different MOS recognized in the presacral axial skeleton of *Europasaurus*, the four main MOS were included in the phylogenetic data matrix (Online Supplementary Material). MOS 4 and 5 of cervical vertebrae were combined because no phylogenetic difference was detected between them (they scored equally for all characters). Thus, MOS 1, MOS 2, MOS 3 and MOS 4 were scored, combining in each MOS the information from cervical and dorsal elements, and treated as different terminals. The analysis was carried out forcing the monophyly of the recovered groups in the MPTs, adding the four MOS, and followed by a constraint search starting from 1000 replicates and saving 10 trees per replicate.

This analysis recovered MOS 1 and MOS 2 in a basal position among sauropods, both being grouped in a clade

with *Cetiosaurus* (as sister taxon to MOS 1 and MOS 2) and *Patagosaurus* as the most basal form (Online Supplementary Material). The absence of the SPDL supports the monophyly of this clade (with a reversion in MOS 2 in which this lamina is slightly developed). As noted above, the presence of the SPDL is a widespread character among sauropods (e.g. Allain & Aquesbi 2008). Therefore, among sauropods, the absence of this lamina could be considered as a product of the retention of a juvenile character, a paedomorphic process in lineages that lack this lamina. The presence of narrow neural spines was recovered as an apomorphic character of *Cetiosaurus* plus MOS 1 and MOS 2. Whereas wider neural spines are widespread among sauropods (e.g. Wilson 2002), narrow neural spines are not usually present, and have been described only for *Jobaria* and *Tehuelchesaurus* (Sereno *et al.* 1999; Carballido *et al.* 2011b). Therefore, the shape of the neural spine in these taxa could be also a result of a paedomorphic process. The monophyly of MOS 1 and MOS 2 is supported by four characters. In these MOS, both SPRL run extremely close to each other, and therefore no wide fossa is present. This morphology mainly resembles the neural spine of basal sauropodomorphs. The second character supporting this assemblage is the presence of opisthocoelous middle and posterior dorsal centra in MOS 1 and MOS 2. This condition is a derived character that evolved twice, in *Mamenchisaurus* + *Omeisaurus*, and in camarasauromorphs. Therefore, its presence in MOS 1 and MOS 2 of *Europasaurus*, and also in the early juvenile sauropod from the Morrison Formation SMA 0009 (Carballido *et al.* 2012a), indicates that this derived character appears early in ontogeny. Additionally, the cervical neural lamination is rudimentary, a plesiomorphic character among sauropods convergently acquired in derived titanosaurs.

In contrast to MOS 1 and MOS 2, MOS 3 and MOS 4 cluster with *Europasaurus* (scored with all the information available) in a monophyletic assemblage. Several characters support this grouping: (1) whereas the cervical vertebrae of MOS 1 and MOS 2 lack pleurocoels (or they are not posteriorly marked), in advanced immature and adult specimens of *Europasaurus*, the pleurocoels are simple, an unusual character among basal macronarian taxa; (2) as noted and discussed above, the posterior notch present in the cervical vertebrae is not a unique autapomorphic character of *Europasaurus* but an unusual character among sauropods; this notch is developed in some way in late immature and, even more so, in mature specimens of *Europasaurus*, and is recovered as a synapomorphy of this group; (3) the presence of a prespinal lamina in cervical vertebrae of late immature and adult specimens, an autapomorphic character of *Europasaurus* convergently acquired in *Isisaurus*, supports the clustering of MOS 3 and 4 with *Europasaurus*; (4) the lateral excavation in the prezygapophyseal process is recovered as a synapomorphic character of *Brachiosaurus* + *Giraffatitan*, convergently acquired in *Europasaurus*; as for the other characters discussed here, these lateral excavations appear in late immature specimens before neurocentral suture closure; and (5) the ventral contact of the SPDL (present since MOS 2) and the SPOL (present in all the MOS) is recovered as a synapomorphy of MOS 3, MOS 4 and *Europasaurus* because it is an unusual character among basal macronarians that normally show more dorsal contact (e.g. *Camarasaurus*; Osborn & Mook 1921).

One of the most interesting results of the analysis presented here is that whereas the presacral region of early immature specimens presents several plesiomorphic characters, placing them in a basal position among sauropods, the phylogenetic information for late mature specimens unequivocally retrieves MOS 3 with adult *Europasaurus*. This implies that before neurocentral closure, but in a late immature stage (such as MOS 3), the morphology of juvenile *Europasaurus* closely resembles that of adult forms (at least for the presacral axial skeleton). Therefore, late juveniles can be regarded as phylogenetically mature (i.e. with the same phylogenetic information observed in adult forms). For the moment it is not known how much this rule can be extended among sauropodomorphs.

The current lack of knowledge on the ontogenetic changes in sauropods makes it extremely difficult to ascertain the systematic affinities of immature material, especially for young immature specimens. Although only a few young immature sauropods are known, the problem is well illustrated by SMA 0009. This nearly complete skeleton, only lacking the skull, was initially described as a diplodocine sauropod (Schwarz *et al.* 2007) but recently reassigned to Brachiosauridae (Carballido *et al.* 2012a). Its axial morphology resembles that described for MOS 1 of *Europasaurus*, in which several plesiomorphic characters obscure the phylogenetic signal. Consequently, the scoring of ontogenetically changing characters and their inclusion in a phylogenetic analysis could push such a specimen down to a more basal position. When the phylogenetic position of a complete specimen is being analysed, this may not be such a problem because many other characters may be ontogeny-independent (e.g. articular surface of centra) and show the 'true' phylogenetic position (Carballido *et al.* 2012a). However, when incomplete specimens, especially those lacking the skull, are being studied, ontogenetically changing characters may be an insurmountable problem. Therefore, the identification of such characters is crucial and should precede the systematic study of such material.

In addition to the changes in fossae development (pneumatic characters), some of the major and more interesting transformations documented for *Europasaurus* are related to changes in neural spine lamination. Thus, particular caution must be exercised when characters of this kind and from this region are scored in juvenile sauropods. On the other hand, neural arch lamination and some features of the centrum are present early in ontogeny, albeit less developed than in adults. Derived centrum characters, such

as the opisthocoelous condition of the cervicals (a synapomorphy of *Amygdalodon* and more derived taxa; Carballido & Pol 2010) and dorsal vertebrae (a synapomorphy of Camarasauromorpha; Salgado *et al.* 1997) or the absence of ventral medial keel in cervical vertebrae (a synapomorphy of *Omeisaurus* and more derived forms; Wilson, 2002), seem to be acquired early in ontogeny.

Morphological ontogenetic stages and histological ontogenetic stages

To be sure that the variation observed between taxa is the result of phylogeny rather than ontogeny, the recognition of mature individuals in the fossil record is important (Brochu 1996). As noted by Queiroz (1985), sexual maturity represents only a single ontogenetic character, so a more comprehensive view of maturity is needed, and this must be based on growth dynamics and the ontogenetic sequence of the appearance of autapomorphies (Irmis 2007). In the preceding section, we discussed how systematic information changes through ontogeny, recognizing that the presacral characters that define the phylogenetic position of *Europasaurus* appear before the closure of the neurocentral suture in late immature specimens (MOS 3). Thus, this can be used as an additional criterion of maturity, which we described as 'phylogenetic maturity'. To widen the maturity criterion, different sources of information should be used and correlated (e.g. phylogenetic maturity, neurocentral fusion and sexual maturity).

As noted by Ikejiri (2012), open neurocentral sutures are traditionally used to identify juvenile dinosaurs, including sauropods (e.g. Tidwell & Carpenter 2003; Schwarz *et al.* 2007). Among vertebrates, the timing of neurocentral fusion varies from the embryonic to the very late postnatal ontogenetic periods; fusion between centra and neural arches even persists in some taxa throughout life (e.g. *Alligator*; Ikejiri 2012). The timing of neurocentral fusion is not known in sauropods. Nevertheless, completely closed neurocentral closures are generally observed among fully grown specimens, and open sutures are observed in juvenile specimens, a morphological change used here to distinguish between juvenile and mature elements.

The preceding description and discussion illustrated some general changes in the axial skeleton through the ontogeny of *Europasaurus*. Some of these changes seem to be the same for other non-diplodocoid sauropods, as similar changes were suggested for *Tazoudasaurus* (Allain & Aquesbi 2008), the brachiosaurid SMA 0009 (Carballido *et al.* 2012a) and *Phuwiangosaurus* (Martin 1994) (e.g. development of the SPDL). Linking these morphological changes, including neurocentral closure, with some measurement of time would be highly desirable. The use of histological ontogenetic stages (HOS; Klein & Sander 2008) in the long bones as a qualitative measure of sauropod age provides an excellent starting point for linking MOS with life history in neosauropods. Still, not enough information exists to correlate directly MOS with HOS because no long bones have been found so far at the Oker locality that are associated with the immature elements described for *Europasaurus.*

Sexual maturity was correlated with HOS 8 by Klein & Sander (2008), in which the animals seem to have reached almost 50% of final size and a marked decrease in growth rate is observed (Sander 2000). In the same individual, the titanosaur *Bonitasaura* shows both completely closed neurocentral sutures and completely disarticulated neural arches, varying along the vertebral column following an anteroposterior direction of neurocentral closure (Gallina 2011). The histology of this sauropod was recently described and assigned to HOS 9 of Klein & Sander (2008; Gallina 2012). This is just one histological ontogenetic stage later than the point of sexual maturity proposed by Klein & Sander. Therefore, it is possible that the neurocentral closure occurs in sauropods between HOS 8 (decrease in growth rate) and 9 (based on the condition of *Bonitasaura*; Gallina 2012) (Fig. 31). If this is correct, it can be assumed that the mature morphological stage of mature vertebrae (with closed neurocentral suture) is older than HOS 8 and that immature vertebrae (with open neurocentral suture) are younger than HOS 9.

Additionally, the early immature stage (MOS 1) of both cervical and dorsal vertebrae may correlate with the HOS 5, because the same morphology was described for the brachiosaurid SMA 0009 (Carballido *et al.* 2012a), which is HOS 5 (Klein & Sander 2008). However, it remains unknown how much earlier or later than HOS 5 the early immature stage began and ended. Taking these observations into account, we suggest that the first two immature stages (MOS 1 and MOS 2) must be placed between HOS 5 and 8, whereas the late immature stage correlates with HOS 7 to HOS 9, with an overlap due to uncertainty regarding the middle immature stage. This argument rests on the observation that the late immature stage in both cervical and dorsal elements shows all the mature characters except neurocentral suture closure, and that the late immature elements are of similar size as some mature vertebrae. It is also to be expected that the major morphological transformations occurred before the decrease in growth rate (around HOS 8; Klein & Sander 2008).

The preliminary correlation made here between morphological and histological ontogenetic stages shows that most of the transformations probably occurred close to HOS 8 in what we define as a late immature stage or MOS 3. At this time, the individuals reached sexual maturity (Klein & Sander 2008) and also acquired all the autapomorphic characters that diagnose adult *Europasaurus*. Thus, juvenile sauropods close to HOS 8 will probably show all the diagnostic characters necessary for a precise systematic assignment to the species level, as was described for MOS 3 of *Europasaurus*.

Size dimorphism in *Europasaurus* vertebrae

Among the *Europasaurus* vertebrae, an unexpected size difference was observed. The anterior cervical vertebra identified as probably the third cervical (DFMMh/FV 991.1) is completely mature (no neurocentral suture was observed on its surface). Nevertheless this element is only around 30% the size of the probable fourth cervical (DFMMh/FV 652.1), which is also mature. The difference in size observed between these two elements must indicate the presence of two animals well differentiated in size. Another clear size difference is observed among the middle cervical vertebrae. The mature element DFMMh/FV 710 (MOS 4) and the two late immature centra DFMMh/FV 554.8 and 785.1 (MOS 3) come from a similar position in the neck. Nevertheless, the immature elements are around 140% the size of the mature vertebra (see Table 1), indicating a suture closure for DFMMh/FV 710 at a much smaller size than in the larger immature specimens. Although these two examples represent the most obvious size dimorphism, several other elements show a similar pattern, including skull elements (Marpmann *et al*. 2011).

Several explanations can be hypothesized for the size dimorphism seen in the vertebrae of *Europasaurus*. Below we provide a brief discussion of some of these, but a longer discussion of this matter will be provided in conjunction with the size dimorphism observed in the skull elements (Marpmann *et al.* 2011). While not as apparent as the size dimorphism in the skull and postcranial axial skeleton, a dimorphism may be reflected in the poor correlation of histological ontogenetic stages versus femur length because, unlike most other sauropods, Klein & Sander (2008) failed to find a good correlation between these two parameters in *Europasaurus*. The initial discovery of the size difference at first prompted the idea of two species being present. However, among the hundreds of sauropod elements collected from the Langenberg Quarry, only three elements were identified as non-*Europasaurus*. These elements can be unequivocally assigned to Diplodocidae and are therefore different from *Europasaurus*. Additionally, and more importantly, all the remaining sauropod material shows the same phylogenetic signal, including several uncommon characters and autapomorphic characters of *Europasaurus* (e.g. cervical vertebrae with a median notch, and the same pleurocoel shape and internal morphology; cervical neural spines with PRSL and POSL). Therefore, all the material was assigned to the same morphospecies. Nevertheless, a more biological differentiation of species cannot be ruled out, as for many if not all morphotaxa. If two species were present they could have been sympatric or separated in time or space. This is because the bone comes from a marine bed about 1 m thick, and we do not know how much time is represented by this bed, or whether the *Europasaurus* bones were transported into the basin from one or more of the surrounding islands (Sander *et al.* 2006).

Sexual dimorphism in a single biological species would be another explanation of extreme individual size variation, although this is uncommon in dinosaurs (Klein & Sander 2008; Sander *et al.* 2011). Sexual dimorphism is poorly known in sauropods, mainly due to the difficulty inherent in its recognition in fossils (Ikejiri 2004; Ikejiri *et al.* 2005).

Conclusions

Unlike other tetrapods, the postcranial axial skeleton of sauropods is regarded as one of the most informative body regions, both because many morphological changes occurred here and also because it is commonly recovered in the fossil record, providing one of the best opportunities for comparing taxa. Here we describe for the first time the complete anatomy of the axial skeleton of juvenile and adult specimens of the dwarf basal camarasauromorph *Europasaurus holgeri*, which provides a wealth of new information on its anatomy and diagnosis. The phylogenetic position of *Europasaurus* was tested through a comprehensive phylogenetic analysis, which includes several basal neosauropods taxa, retrieving *Europasaurus* as a basal camarasauromorph, a position that compares well with previous analyses and shows good branch support. The analysis also contributes to a better understanding of the early evolution of macronarian sauropods. Nevertheless, the low support obtained in most of macronarian branches indicates that some uncertainty exists in the early evolutionary stages of this group.

Despite the enormous ontogenetic size range, ontogenetic changes in sauropods are poorly known, mainly due to the absence of young specimens. The description and comparison of juvenile specimens with adults of *Europasaurus* provides, for the first time, a wealth of information on the ontogenetic changes in the axial skeleton, which probably can be extended to a more inclusive group of sauropods because similar changes were observed in basal sauropods (e.g. *Tazoudasaurus*) and more derived macronarians (e.g. SMA 0009; *Phuwiangosaurus*). The most drastic of these changes includes the absence of derived characters in early morphological stages, for example, the absence of SPDL and PRSL laminae in dorsal vertebrae, but the presence of some derived characters such as the opisthocoelous condition of such vertebrae. The presence of derived and autapomorphic characters before the neurocentral closure indicates that 'phylogenetic maturity' is reached before morphological maturity, and probably before sexual maturity. Therefore, whereas late immature specimens can be assigned unequivocally to *Europasaurus*, earlier juveniles provide an incorrect phylogenetic signal. The use of size-independent characters for determining the ontogenetic stages allowed us to recognize two well-differentiated size classes, which may either represent sexual morphs or different biological species separated in time or space.

Acknowledgements

We especially want to thank N. Knötschke for complete access to and preparation of the material. Comments and suggestions made by L. Salgado, D. Pol, K. Stein and S. Marpmann and other members of the Bonn working group during the preparation of this manuscript are greatly appreciated. Jessica Mitchell is thanked for English corrections. Comments made by P. Mannion, an anonymous reviewer and the editor helped improve an early version of this paper. The authors gratefully acknowledge the financial support provided by the Deutsche Forschungsgemeinschaft (DFG) for this research (Project RE 2874/1–1 and SA 469/33–1), and FoncyT PICT 2006–1756 (to D. Pol). This paper is contribution number 134 of the DFG Research Unit 533 'Biology of the Sauropod Dinosaurs: The Evolution of Gigantism'. Comparisons with relevant material was possible thanks to the collection access provided by: R. Coria (MCF-PVPH); A. Kramarz (MACN); E. Ruigomez (MEF); A. Garrido (MOZ); J. Calvo and J. Porfiri (MUCPv); J. Powell (PVL); L. Giraldez (CHMO); B. González Riga, (IANIGLA); I. Cerda (MCS); R. Royo Torres (MPZ, CPT, CL and CLH); O. Mateus (MIGM and ML); B. Pabst and S. Hans-Jakob (SMA); J. Nour-Eddine (CPSGM); N. Knötschketo (DFMMh); D. Schwarz and F. Witzmann (HMN); J. Ove R. Ebbestad (PMU); F. Torcida (MPS-RV-II); B. Battail (MNHN); X. Xu (IVPP); G. Peng and S. Jiang (ZDM); C. Ito and M. Brett-Surman (USNM); W. F. Simpson (FMNH); A. Henrici (CM); and J. Canale and A. Haluza (MMCH).

Supplementary material

Supplementary material is available online DOI: 10.1080/14772019.2013.764935

References

Allain, R. & **Aquesbi, N.** 2008. Anatomy and phylogenetic relationships of *Tazoudasaurus naimi* (Dinosauria, Sauropoda) from the late Early Jurassic of Morocco. *Geodiversitas*, **30**, 345–424.

Antunes, M. T. & **Mateus, O.** 2003. Dinosaurs of Portugal. *Comptes Rendus Palevol*, **2**, 77–95.

Apesteguía, S. 2005. The evolution of the hyposphene–hypantrum complex within Sauropoda. Pp. 248–267 in V. Tidwell & K. Carpenter (eds) *Thunder-Lizards: the Sauropodomorph Dinosaurs*. Indiana University Press, Indianopolis.

Bonaparte, J. F. 1986. Les dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétiosauridés) du Jurassique moyen de Cerro Cóndor (Chubut, Argentina). *Annales de Paléontologie*, **72**, 325–386.

Bonaparte, J. F. 1996. Cretaceous tetrapods of Argentina. Pp. 73–130 in G. Arratia (ed.) *Contributions of southern South America to Vertebrate Paleontology*. Münchner Geowissenschaftliche Abhandlungen (A), Munich.

Bonaparte, J. F. 1999. Evolución de las vértebras presacras en Sauropodomorpha. *Ameghiniana*, **36**, 115–187.

Brinkman, D. 1988. Size-independant criteria for estimating relative age in Ophiacodon and Dimetrodon (Reptilia, Pelycosauria) from the Admiral and Belle Plains Formations of west-central Texas. *Journal of Vertebrate Paleontology*, **8**, 172–180.

Brochu, C. A. 1996. Closure of neurocentral sutures during crocodilian ontogeny: implications for maturity assessment in fossil archosaurs. *Journal of Vertebrate Paleontology*, **16**, 49–62.

Buffetaut, E., Suteethorn, V., Cuny, G., Tong, H., Le Loeuff, J., Khansubha, S. & **Jongautchariyakul, S.** 2000. The earliest known sauropod dinosaur. *Nature*, **407**, 72–74.

Calvo, J., Porfiri, J., González Riga, B. J. & **Kellner, A. W.** 2007. A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new sauropod dinosaur. *Anais da Academia Brasileira de Ciências*, **79**, 529–541.

Campos, D. A., Kellner, A. W. A., Bertini, R. J., & Santucci, R. M. 2005. On a titanosaurid (Dinosauria, Sauropoda) vertebral column from the Bauru Group, Late Cretaceous of Brazil. *Arquivos do Museu Nacional, Rio de Janeiro*, **63**: 565–593.

Canudo, J. I., Royo Torres, R. & **Cuenca-Bescós, G.** 2008. A new sauropod: *Tastavinsaurus sanzi* gen. et sp. nov. from the Early Cretaceous (Aptian) of Spain. *Journal of Vertebrate Paleontology*, **28**, 712–731.

Carballido, J. L. & **Pol, D.** 2010. The dentition of *Amygdalodon patagonicus* (Dinosauria: Sauropoda) and the dental evolution in basal sauropods. *Comptes Rendus Palevol*, **9**, 83–93.

Carballido, J. L., Pol, D., Cerda, I. & **Salgado, L.** 2011a. The osteology of *Chubutisaurus insignis* Del Corro, 1975 (Dinosauria: Neosauropoda) from the "middle" Cretaceous of central Patagonia, Argentina. *Journal of Vertebrate Paleontology*, **31**, 93–110.

Carballido, J. L., Rauhut, O. W. M., Pol, D. & **Salgado, L.** 2011b. Osteology and phylogenetic relationships of *Tehuelchesaurus benitezii* (Dinosauria, Sauropoda) from the Upper Jurassic of Patagonia. *Zoological Journal of the Linnean Society of London*, **163**, 605–662.

Carballido, J., Marpmann, J., Schwarz-Wings, D. & **Pabst, B.** 2012a. New information on a juvenile sauropod specimen from the Morrison Formation and the reassessment of its systematic position. *Palaeontology*, **55**, 567–582.

Carballido, J. L., Salgado, L., Pol, D., Canudo, J. I. & **Garrido, A.** 2012b. A new basal rebbachisaurid (Sauropoda, Diplodocoidea) from the Early Cretaceous of the Neuquén Basin; evolution and biogeography of the group. *Historical Biology*, **24**, 631–654.

Carpenter, K. & **McIntosh, J.** 1994. Upper Jurassic sauropod babies from the Morrison Formation. Pp. 265–278 in K. Carpenter, K. F. Hirsch & J. R. Horner (eds) *Dinosaur eggs and babies*. Cambridge University Press, Cambridge.

Chure, D., Britt, B., Whitlock, J. A. & **Wilson, J. A.** 2010. First complete sauropod dinosaur skull from the Cretaceous of the Americas and the evolution of sauropod dentition. *Naturwissenschaften*, **97**, 379–391.

Curry Rogers, K. A. 2009. The postcranial osteology of Rapetosaurus krausei (Sauropoda: Titanosauria) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology*, **29**, 1046–1086.

Cope, E. D. 1877. On a gigantic saurian from the Dakota epoch of Colorado. *Paleontological Bulletin*, **25**, 5–10.

Foster, J. R. 2005. New juvenile sauropod material from western Colorado, and the record of juvenile sauropods from the Upper Jurassic Morrison Formation. Pp. 141–153 in V. Tidwell & K. Carpenter (eds) *Thunder-Lizards. The Sauropodomorph*

Dinosaurs. Indiana University Press, Bloomington and Indianapolis.

Fraas, E. 1908. Ostafrikanische Dinosaurier. *Palaeontographica*, **55**, 105–144.

Gallina, P. A. 2011. Notes on the axial skeleton of the titanosaur *Bonitasaura salgadoi* (Dinosauria-Sauropoda). *Annals of the Brazilian Academy of Sciences*, **83**, 235–246.

Gallina, P. A. 2012. Histología ósea del titanosaurio *Bonitasaura salgadoi* (Dinosauria: Sauropoda) del Cretácico Superior de Patagonia. *Ameghiniana*, **49**, 289–302.

Galton, P. M. 2001. The prosauropod dinosaur Plateosaurus Meyer, 1837 (Saurischia; Sauropodomorpha; Upper Triassic). II. Notes on the referred species. *Revue de Paláobiologie*, **20**, 435–502.

Gilmore, C. W. 1925. A nearly complete articulated skeleton of *Camarasaurus*, a saurischian dinosaur from the Dinosaur National Monument, Utah. *Memoirs of the Carnegie Museum. Proceedings of the US National Museum*, **81**, 1–21.

Goloboff, P. A., Farris, S. & **Nixon, K.** 2008a. TNT, a free program for phylogenetic analysis. *Cladistics*, **24**, 774–786.

Goloboff, P. A., Farris, S. & **Nixon, K.** 2008b. TNT: Tree analysis using New Technology, vers. 1.1 (Will Henning Society Edition). Updated at: http://www.zmuc.dk/public/phylogeny/tnt., accessed 3 March 2012.

Gomani, E. M. 2005. Sauropod dinosaurs from the Early Cretaceous of Malawi, Africa. *Palaeontologia Electronica*, **1**, 37 pp.

González Riga, B. J. 2005. Nuevos restos fósiles de *Mendozasaurus neguyelap* (Sauropoda, Titanosauria) del Cretácico Tardío de Mendoza, Argentina. *Ameghiniana*, **42**, 535–548.

González Riga, B. J., Previtera, E. & **Pirrone, C.** 2009. *Malarguesaurus florenciae* gen. et sp. nov., a new titanosauriform (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza, Argentina. *Cretaceous Research*, **30**, 135–148.

Griebeler, E. M. & **Werne, J.** 2011. The life cycle of sauropod dinosaurs. Pp. 263–275 in N. Klein, K. Remes, C. T. Gee & P. M. Sander (eds) *Biology of the Sauropod Dinosaurs: Understanding the Life of Giants*. Inidana University Press, Bloomington and Indianapolis.

Harris, J. D. 2006. The significance of *Suuwassea emilieae* (Dinosauria: Sauropoda) for flagellicaudatan intrarelationships and evolution. *Journal of Systematic Palaeontology*, **4**, 185–198.

Hatcher, J. B. 1903. Osteology of *Haplocanthosaurus* with description of a new species, and remarks on the probable habits of the Sauropoda, and the age and origin of the *Atlantosaurus* beds. Aditional remarks on *Diplodocus*. *Memoirs of the Carnegie Museum*, **2**, 1–75.

He, X., Yang, S., Cai, K. & **Liu, Z.** 1996. A new species of sauropod *Mamenchisaurus anyuensis* sp. nov. *Proceedings of the 30th International Geological Congress*, **12**, 83–86.

Ikejiri, T. 2003. Sequence of closure of neurocentral sutures in *Camarasaurus* (Sauropoda) and implications for phylogeny in Reptilia. *Journal of Vertebrate Paleontology*, **23**, 65A.

Ikejiri, T. 2004. Relative growth and timing of ontogenetic changes in *Camarasaurus* (Dinosauria Sauropoda). *Journal of Vertebrate Paleontology*, **24**, 74A.

Ikejiri, T. 2012. Histology-based morphology of the neurocentral synchondrosis in *Alligator mississippiensis* (Archosauria, Crocodylia). *The Anatomical Record*, **295**, 18–31.

Ikejiri, T., Tidwell, V. & **Trexler, D. L.** 2005. New adult specimen of *Camarasaurus lentus* highlight ontogenetic variation within the species. Pp. 154–179 in V. Tidwell & K. Carpenter (eds) *Thunder-Lizards. The Sauropodomorph Dinosaurs.* Inidana University Press, Bloomington and Indianapolis.

Irmis, R. B. 2007. Axial skeleton ontogeny in the Parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs. *Journal of Vertebrate Paleontology*, **27**, 350–361.

Janensch, W. 1947. Pneumatizitat bei Wirbeln von Sauropoden und anderen Saurischien. *Palaeontographica (Suppl. 7)*, **3**, 1–25.

Janensch, W. 1914. Übersicht über die Wirbeltierfauna der Tendaguru-Schichten, nebst einer kurzen Charakterisierung der neu aufgestellten Arten von Sauropoden. *Archiv fur Biontologie*, **3**, 81–110.

Janensch, W. 1950. Die Wirbelsäule von *Brachiosaurus brancai*. *Palaeontographica (Suppl. 7)*, **3**, 27–93.

Kearney, M. & **Clark, J. M.** 2003. Problems due to missing data in phylogenetic analyses including fossils: a critical review. *Journal of Vertebrate Paleontology*, **23**, 263–274.

Klein, N. & **Sander, M.** 2008. Ontogenetic stages in the long bone histology of sauropod dinosaurs. *Paleobiology*, **34**, 247–263.

Klein, N., Sander, P. M., Stein, K., Le Loeuff, J., Carballido, J. L. & **Buffetaut, E.** 2012. Modified laminar bone in *Ampelosaurus atacis* and other titanosaurs (Sauropoda): Implications for life history and physiology. *PLoS ONE*, **7**, e36907.

Ksepka, D. T. & **Norell, M. A.** 2010. The illusory evidence for Asian Brachiosauridae: New material of *Erketu ellisoni* and a phylogenetic reappraisal of basal Titanosauriformes. *American Museum Novitates*, **3700**, 1–27.

Lapparent, A. F. & **Zbyszywski, G.** 1957. Les dinosauriens du Portugal. *Memoires des Services Géologiques du Portugal*, **2**, 1–63.

Maddison, W. P. & **Maddison, D. R.** 2011. *Mesquite: a modular system for evolutionary analysis*. Version 2.74. Updated at http://mesquiteproject.org, accessed 30 September 2011.

Madsen, J. H., McIntosh, J. S. & **Berman, D. S.** 1995. Skull and atlas–axis complex of the Upper Jurassic sauropod *Camarasaurus* Cope (Reptilia: Saurischia). *Bulletin of the Carnegie Museum of Natural History*, **31**, 1–115.

Mannion, P. D. 2011. A reassessment of *Mongolosaurus haplodon* Gilmore, 1933, a titanosaurian sauropod dinosaur from the Early Cretaceous of Inner Mongolia, People's Republic of China. *Journal of Systematic Palaeontology*, **9**, 355–378.

Mannion, P. D. & **Calvo J. O.** 2011. Anatomy of the basal titanosaur (Dinosauria, Sauropoda) *Andesaurus delgadoi* from the mid-Cretaceous (Albian–early Cenomanian) Río Limay Formation, Neuquén Province, Argentina: implications for titanosaur systematics. *Zoological Journal of the Linnean Society*, **163**, 155–181.

Mannion, P. D., Upchurch, P. & **Hutt, S.** 2011a. New rebbachisaurid (Dinosauria: Sauropoda) material from the Wessex Formation (Barremian, Early Cretaceous), Isle of Wight, United Kingdom. *Cretaceous Research*, **32**, 774–780.

Mannion, P. D., Upchurch, P., Carrano, M. T. & **Barrett, P. M.** 2011b. Testing the effect of the rock record on diversity: a multidisciplinary approach to elucidating the generic richness of sauropodomorph dinosaurs through time. *Biological Reviews*, **86**, 157–181.

Mannion, P. D., Upchurch, P., Mateus, O., Barnes, R. & **Jones, M. E. H.** 2012. New information on the anatomy and systematic position of *Dinheirosaurus lourinhanensis* (Sauropoda: Diplodocoidea) from the Late Jurassic of Portugal, with a review of European diplodocoids. *Journal of Systematic Palaeontology*, **10**, 521–551.

Martin, V. 1994. Baby sauropods from the Sao Khua Formation (Lower Cretaceous) in northeastern Thailand. *Gaia, Lisboa*, **10**, 147–153.

Marpmann, J. S., Carballido, J., Remes, K., & Sander, P. 2011. Ontogenetic changes in the skull elements of the Late Jurassic Dwarf sauropod *Europasaurus holgeri*. *Journal of Vertebrate Paleontology*, **31**(Supplement to no. 6), 151A.

Marsh, O. C. 1878. Principal characters of American Jurassic dinosaurs. Pt. I. *American Journal of Science*, **16**, 411–416.

Marsh, O. C. 1895. On the affinities and classification of the dinosaurian reptiles. *American Journal of Science, Series 3*, **50**, 483–498.

McIntosh, J. S., Miller, W. E., Stadtman, K. L. & **Gillette, D. C.** 1996. The osteology of *Camarasaurus lewisi* (Jensen, 1988). *Brigham Young University, Geology Studies*, **41**, 73–115.

Müller, J., Scheyer, T. M., Barrett, P. M., Werneburg, I., Head, J. J., Ericson, P. G. P., Pol, D. & **Sanchez-Villagra, M. R.** 2010. The evolution of vertebral numbers in recent and fossil amniotes: The roles of homeotic effects and somitogenesis. *Proceedings of the National Academy of Sciences USA*, **107**, 2118–2123.

Nixon, K. & **Wheeler, Q. D.** 1992. The parsimony ratchet: a new method for rapid parsimony analysis. *Cladistics*, **15**, 407–414.

Osborn, H. F. & **Mook, C. C.** 1921. *Camarasaurus, Amphicoelias* and other sauropods of Cope. *Memoirs of the American Museum of Natural History*, **3**, 247–387.

Otero, A., Gallina, P. A., Canale, J. I. & **Haluza, A.** 2012. Sauropod haemal arches: morphotypes, new classification and phylogenetic aspects. *Historical Biology*, **24**, 243–256.

Pol, D. & **Escapa, I.** 2009. Untestable taxa in cladistic analysis: identification and the assessment of relevant characters. *Cladistics*, **25**, 515–527.

Pol, D., Garrido, A. C. & **Cerda, I. A.** 2011. A new sauropodomorph dinosaur from the Early Jurassic of patagonia and the origin and evolution of the sauropod-type sacrum. *PLoS ONE*, **6**, e14572.

Powell, J. E. 2003. Revision of South American titanosaurid dinosaurs: palaeobiological, palaeobiogeographical and phylogenetic aspects. *Records of the Queen Victoria Museum*, **111**, 1–173.

Queiroz, K. 1985. The ontogenetic method for determining character polarity and its relevance to phylogenetic systematics. *Systematic Zoologist*, **34**, 280–299.

Reisz, R. R., Evans, D. C., Sues, H.-D. & **Scott, D.** 2010. Embryonic skeletal anatomy of the sauropodomorph dinosaur *Massospondylus* from the Lower Jurassic of South Africa. *Journal of Vertebrate Paleontology*, **30**, 1653–1665.

Remes, K. 2007. A second gondwanan diplodocid dinosaur from the Upper Jurassic Tendaguru beds of Tanzania, East Africa. *Palaeontology*, **50**, 653–667.

Riggs, E. S. 1903. *Brachiosaurus altithorax*, the largest known dinosaur. *American Journal of Science, Series 4*, **15**, 299–306.

Riggs, E. S. 1904. Structure and relationships of opisthocoelian dinosaurs. Part II, the Brachiosauridae. *Field Columbian Museum, Geological Series*, **2**, 229–247.

Rose, P. J. 2007. A new titanosauriform sauropod (Dinosauria: Saurischia) from the Early Cretaceous of central Texas and its phylogenetic relationships. *Palaeontologica Electronica*, **10**, 1–65.

Salgado, L. & **Bonaparte, J. F.** 1991. Un nuevo sauropodo Dicraeosauridae, Amargasaurus cazaui gen. et sp. nov., de la Formacin La Amarga, Neocomiano de la Provincia del Neuquén, Argentina. *Ameghiniana*, **28**, 333–346.

Salgado, L. & **Powell, J. E.** 2010. Reassessment of the vertebral laminae in some South American titanosaurian sauropods. *Journal of Vertebrate Paleontology*, **30**, 1760–1772.

Salgado, L., Coria, R. A. & **Calvo, J. O.** 1997. Evolution of titanosaurid sauropods. I: Phylogenetic analysis based on the postcranial evidence. *Ameghiniana*, **34**, 3–32.

Salgado, L., García, R. A. & **Daza, D.** 2006. Consideraciones sobre las láminas neuronales de los dinosaurios saurópodos y su significado morfofuncional. *Revista del Museo Argentino de Ciencias Naturales*, **81**, 69–79.

Salgado, L., Garrido, A. C., Cocca, S. E. & **Cocca, J. R.** 2004. Lower Cretaceous rebbachisaurid sauropods from Cerro Aguada Del León, Neuquén Province, northwestern Patagonia, Argentina. *Journal of Vertebrate Paleontology*, **24**, 903–912.

Sander, P. M. 2000. Longbone histology of the Tendaguru sauropods: implications for growth and biology. *Paleobiology*, **26**, 466–488.

Sander, M. P., Mateus, O., Laven, T. & **Knötschke, N.** 2006. Bone histology indicates insular dwarfism in a new Late Jurassic sauropod dinosaur. *Nature*, **441**, 739–741.

Sander, M. P., Peitz, C., Jackson, F. D. & **Chiappe, L. M.** 2008. Upper Cretaceous titanosaur nesting sites and their implications for sauropod dinosaur reproductive biology. *Palaeontographica*, **284**, 69–107.

Sander, M. P., Klein, N., Stein, K. & **Wings, O.** 2011. Sauropod bone histology and its implications for sauropod biology. Pp. 276–302 in N. Klein, K. Remes, C. Gee & M. P. Sander (eds) *Biology of the Sauropod Dinosaurs: Understanding the Life of Giants*. Indiana University Press, Bloomington and Indianapolis.

Schwarz, D., Ikejiri, T., Breithaupt, B. H., Sander, M. P. & **Klein, N.** 2007. A nearly complete skeleton of an early juvenile diplodocid (Dinosauria: Sauropoda) from the Lower Morrison Formation (Late Jurassic) of north central Wyoming and its implications for early ontogeny and pneumaticity in sauropods. *Historical Biology*, **19**, 225–253.

Seeley, H. G. 1887. On the classification of the fossil animals commonly called Dinosauria. *Proceedings of the Royal Society of London*, **43**, 165–171.

Sereno, P., Beck, A. L., Dutheil, D. B., Larsson, H. C. E., Lyon, G. H., Moussa, B., Sadleir, R. W., Sidor, C. A., Varricchio, D. J., Wilson, G. P., & Wilson, J. A. 1999. Cretaceous sauropods from the Sahara and the Uneven Rate of skeletal evolution among dinosaurs. *Science*, **286**, 1342–1347.

Stein, K., Csiki, Z., Rogers, K., Weishampel, D., Redelstorff, R., Carballido, J. & **Sander, M.** 2010. Small body size and extreme cortical bone remodeling indicate phyletic dwarfism in *Magyarosaurus dacus* (Sauropoda: Titanosauria). *Proceedings of the National Academy of Sciences, USA*, **107**, 9258–9263.

Suteethorn, S., Le Loeuff, J., Buffetaut, E. & **Suteethorn, V.** 2010. Description of topotypes of *Phuwiangosaurus sirindhornae*, a sauropod from the Sao Khua Formation (Early Cretaceous) of Thailand, and their phylogenetic implications. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **256**, 109–121.

Taylor, M. P. 2009. A re-evaluation of *Brachiosaurus altithorax* Riggs 1903 (Dinosauria, Sauropoda) and its generic separation from *Giraffatitan brancai* (Janensch 1914). *Journal of Vertebrate Paleontology*, **29**, 787–806.

Tidwel, V., & Carpenter, K. 2003. Braincase of an early Cretaceous titonosauriform sauropod from Texas. *Journal of Vertebrate Paleontology*, **23**, 176–180.

Tidwell, V. & **Wilhite, D. R.** 2005. Ontogenetic variation and isometric growth in the forelimb of the Early Cretaceous sauropod *Venenosaurus*; pp. 187–198 in V. Tidwell, & K. Carpenter (eds) *Thunder Lizards: the Sauropodomorph*

Dinosaurs. Indiana University Press, Bloomington and Indianapolis.

Upchurch, P. 1995. The evolutionary history of sauropod dinosaurs. *Philosophical Transactions of the Royal Society of London, Series B*, **349**, 365–390.

Upchurch, P. 1998. The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society of London*, **124**, 43–103.

Upchurch, P. & **Martin, J. E.** 2002. The Rutland *Cetiosaurus*: the anatomy and relationships of a Middle Jurassic British sauropod dinosaur. *Palaeontology*, **45**, 1049–1074.

Upchurch, P., & Martin, J. 2003. The anatomy and taxonomy of Cetiosaurus (Saurischia: Sauropoda) from the Middle Jurassic of England. *Journal of Vertebrate Paleontology*, **23**, 208–231.

Upchurch, P., Barret, P. M. & **Dodson, P.** 2004. The sauropods. Pp. 259–354 in D. B. Weishampel, P. Dodson & H. Osmólska (eds) The Dinosauria. 2nd Edition. University of California Press, Berkeley.

Upchurch, P., Mannion, P. D., Benson, R. B. J., Butler, R. J. & **Carrano, M. T.** 2011. Geological and anthropogenic controls on the sampling of the terrestrial fossil record: A case study from the dinosauria. *Geological Society Special Publication*, **358**, 209–240.

Varricchio, D. J. 1997. Growth and embryology. Pp. 282–288 in P. J. Currie & K. Padian (eds) *Encyclopedia of Dinosaurs*. Academic Press, London.

Wedel, M. J. 2003. The evolution of vertebral pneumaticity in sauropods dinosaurs. *Journal of Vertebrate Paleontology*, **23**, 344–357.

Wedel, M. J. 2009. Evidence for bird-like air sacs in saurischian dinosaurs. *Journal of Experimental Zoology*, **311**, 611–628.

Werner, J. & **Griebeler, E. M.** 2011. Reproductive biology and its impact on body size: comparative analyses of mammalian, avian and dinosaurian reproduction. *PLoS ONE*, **6**, e28442.

Whitlock, J. A. 2011. A phylogenetic analysis of Diplodocoidea (Saurischia: Sauropoda). *Zoological Journal of the Linnean Society of London*, **161**, 872–915.

Wilson, J. A. 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *Journal of Vertebrate Paleontology*, **19**, 639–653.

Wilson, J. A. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zoological Journal of the Linnean Society of London*, **136**, 215–275.

Wilson, J. A. 2011. Anatomical terminology for the sacrum of sauropod dinosaurs. *Contributions from the Museum of Paleontology, University of Michigan*, **32**, 59–69.

Wilson, J. A. & **Sereno, P. C.** 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Memoirs of the Society of Vertebrate Paleontology*, **5**, 1–68.

Wilson, J. A. & **Upchurch, P.** 2003. A revision of *Titanosaurus* Lydekker (Dinosauria – Sauropoda), the first dinosaur genus with a "Gondwanan" distribution. *Journal of Systematic Palaeontology*, **1**, 125–160.

Wilson, J. A. & **Upchurch, P.** 2009. Redescription and reassessment of the phylogenetic affinities of *Euhelopus zdanskyi* (Dinosauria: Sauropoda) from the Early Cretaceous of China. *Journal of Systematic Palaeontology*, **7**, 199–239.

Wilson, J. A., D'Emic, M. D., Ikejiri, T., Moacdieh, E. M. & **Whitlock, J. A.** 2011. A Nomenclature for vertebral fossae in sauropods and other saurischian dinosaurs. *PLoS ONE*, **6**, e17114.

Woodruff, D. C. & **Fowler, D. W.** 2012. Ontogenetic influence on neural spine bifurcation in diplodocoidea (dinosauria: Sauropoda): A critical phylogenetic character. *Journal of Morphology*, **273**, 754–764.

Woodward, H. & **Lehman, T.** 2009. Bone histology of the sauropod dinosaur *Alamosaurus sanjuanensis* from the Javelina Formation, Texas. *Microscopy and Microanalysis*, **13**, 508–509.

Yates, A. M. & **Kitching, J. W.** 2003. The earliest known sauropod dinosaur and the first steps towards sauropod locomotion. *Proceedings of the Royal Society of London, Series B*, **270**, 1753–1758.